

D. osana Armbruster: Burger & Liesner 7278, Burger & Gentry 8962, 9011 B, Gomez 19672, Liesner 1869, Utley & Utley 1214 (F).

D. parvibracteata Lanj.: Jenman 4088 (US); McDowell & Gopaul 2264 (ALA, US). *D. parvifolia* Lam.: Armbruster et al. 90-168, Armbruster & Steiner 90-195 (ALA). *D. pentaphylla* Lam.: Hatschbach 11840, Mexia 4149, Regnelli 1051 (F); Webster et al. 25215 (ALA); Woytkowski 35147 (F).

D. scandens L.: Alexandre 227 (CAY); Armbruster & Herzig 85-107, 85-124, Armbruster et al. 87-103, 87-107, 87-115, 87-140 (ALA); Benoist 835, 1262 (P); Billiet & Jadin 4332 (BM, CAY); Broadway 444 (US); Cremers & Hoff 10608, Feuillet 538, 2969 (CAY); Gentry & Revilla 16246, Gentry et al. 22702 (MO); Gillespie & Persaud 1046, Gillespie et al. 1654, 1655, 1781 (ALA, US); Granville 6940 (B, CAY, P); Harrison 714 (K); Harrison 1769 (K, NY); Hekking 1049 (U); Hitchcock 16770, Irwin BG-71 (US); Irwin et al. 55831 (MO, NY, U, US); Kappler 1888 (P, U); Lall 312 (U); Lanjouw & Lindeman 1114, 1807 (NY, U); L.B.B. (J.T. Serringa) 12534 (U); Maas et al. 7222 (B, US); Prevost 1456 (CAY); Reitsma & Reitsma 852 (NY); Sagot 512 (BM, P); Schomburgk 610 (BM); Service Forestier 3077 (U); Service Forestier 4328 (CAY, P, U); Skog et al. 7427 (CAY, NY, P, U, US); Solomon 8899 (MO); Solomon & Escobar 12486 (ALA, MO); Wachenheim 25 (P); Webster 24143 (NY, U); Webster & Armbruster 23508, 23523, 25105 (ALA). *D. schippii* Standley: Armbruster 77-303, 78-416, 79-204 (ALA). *D. schottii* Greenm.:

Armbruster 77-305, 78-409 (ALA). *D. shankii* (Molina) Huft: Armbruster 79-213, 91-102, Armbruster & Berg 85-128 (ALA); Cuatrecasas 21512, Davidson 6828, Shank & Molina 4427, 4475, Standley & Valerio 48588 (F). *D. spathulata* Baill.: Croat 20306, Poeppig 2380, Vigo 6480, 7693 (MO); Williams 4189 (F). *D. subternata* Muell. Arg.: Armbruster et al. 90-144, 90-150, Armbruster & Hines 90-158, 90-160, 90-162, 90-164 (ALA); Croat 30708, 30744, 31022, 31065, Dorr 3050, Gentry 11801 (MO); Gillespie 4180, 4181 (ALA, US); Lorence 2097 (MO); Miller & Keating 4527, Phillipson 2492, 3050 (ALA, MO).

D. tiliifolia Lam.: Armbruster et al. 85-108, 85-111, 87-111, 87-125, 87-138, 87-141 (ALA); Barthelemy 145 (CAY); Broadway 631 (NY); Cremers 9429 (B, CAY, MO, NY, P, US); Feuillet 1754 (CAY, P); Forest Dept. Brit. Guy. 5978 (K, NY); Granville 260 (CAY, P, U); Granville 265 (CAY); Hoff 5357 (B, CAY, NY, P, US); Mori et al. 15026 (CAY, P); Oldeman B-802 (CAY, U); Picon et al. 1524 (ALA, VEN); Poncy 4 (P); Prevost 1808 (CAY, U, US); Sagot 513 (P); Solomon 3248, 7586 (MO); Webster & Armbruster 23712 (ALA). *D. triphylla* Lam.: Armbruster & Herzig 85-103 (ALA); Barreto 5058, Henschen 1052 (F); Webster & Armbruster 25182, 25189, 25218 (ALA).

Plukenetia spp.: Armbruster 78-420, Armbruster et al. 85-106, 87-110, 87-113, 87-144, Webster & Armbruster 23412 (ALA).

Tragia spp.: Armbruster et al. 90-146, Armbruster & Hines 90-157, 90-159, 90-163 (ALA); Maas 6231 (MO).

POLLEN MORPHOLOGY AND PHYLOGENY OF THE TRIBE PLUKENETIEAE (EUPHORBIACEAE)¹

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ABSTRACT

A scanning electron microscopy and light microscopy survey of pollen morphology in the Plukenetieae (Euphorbiaceae) was undertaken to help elucidate phylogenetic relationships within the tribe. Pollen is medium to large, spheroidal to suboblate, and tricolpate, inaperturate, or with poorly defined apertures. Subtribe Plukenetiinae is characterized by tricolpate pollen with uneven-margined colpi and a perforate to reticulate tectum. Pollen evidence supports a division between genera having an aborescent habit (*Angostyles*, *Astrococcus*, and *Haematostemon*) and those with a scandent habit (*Plukenetia* and *Romanoa*). The synonymy of the monotypic genera *Vigia* and *Eleuthero stigma* with *Plukenetia* is also supported. Subtribe Tragiinae is exceptionally diverse in pollen morphology. Aperture condition ranges from tricolpate, the plesiomorphic and most common state, to weakly aperturate and inaperturate; islands, fragments, or strands of sexine are usually present on the apertural membrane, and aperture margins are uneven and often indistinct. Exine sculpture is punctate, foveolate, reticulate, rugulate, or baculate. The large genus *Tragia* includes seven distinct pollen types, with most sections (e.g., *Bia*, *Ctenomeria*, *Leptobotrys*, *Tragia*, and *Zuckertia*, and also subgenus *Mauroya*) characterized by a uniform and unique pollen morphology, supporting the sectional classification of *Tragia*. The other Tragiinae genera have pollen distinct from *Tragia*, with the exception of *Tragiella*, which closely resembles sections *Tagira* and *Lassia*. Pollen evidence supports *Cnesmone* and *Megistostigma* as sister taxa, and suggests a close relationship with *Pachystylidium*. *Acidoton* includes two different pollen types; the inaperturate type closely resembles pollen of *Platygyne*, suggesting that *Acidoton* may not be monophyletic and the tricolpate species perhaps represents a distinct genus. Pollen, together with floral morphological evidence, supports the hypothesis of section *Zuckertia* as a plesiomorphic member of *Tragia*, and suggests that *Tragia* is paraphyletic and that the smaller Tragiinae genera are derived from *Tragia*.

The Plukenetieae belong to the Acalyphoideae, the largest and least understood of the five euphorbiaceous subfamilies. The tribe includes 13 genera distributed worldwide in tropical and warm temperate regions. Many species are twining vines or lianas, both unusual habits in the family; other species are erect herbs, shrubs, or rarely small trees. Although flowers are small and apetalous, floral morphology is diverse, particularly the style and androecium. Another uncommon feature is the presence of stinging hairs in many species. *Tragia* L. is the largest genus, with more than 125 species, some of which are commonly known as nose burns. All other genera have fewer than 17 species each; many are monotypic or with few species. Circum-

scription of genera and infratribal phylogenetic relationships are the principal systematic problems in the Plukenetieae.

Pollen morphology has been invaluable in the systematics of the Euphorbiaceae (Punt, 1962; Köhler, 1965). Light microscopic (LM) observations by Punt (1962), in his pollen survey of the Euphorbiaceae, revealed a diversity of pollen types among species belonging to the Plukenetieae. The present study of pollen morphology of the Plukenetieae based on scanning electron microscopy (SEM) and LM was initiated to help resolve problems of generic circumscription and elucidate phylogenetic relationships. The study is the first part of a larger project concerning the evolutionary

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history of the Plukenetieae, which will include cladistic analyses based on floral, vegetative, and other characters, studies of trends in character evolution, and an attempt at correlating the unusual and often bizarre diversity in floral morphology with pollination biology. Determining plesiomorphic character states and the direction of evolutionary trends will also be of importance in phylogenetic studies of other genera for which the Plukenetieae or its members have been considered as outgroup(s), such as *Dalechampia* L. (Armbruster, 1994) and *Omphalea* L. (Gillespie, 1988).

There have been many additions and taxonomic changes in the Plukenetieae since it was first recognized as a distinct group by Bentham (1880, as subtribe "Plukenetieae"). The circumscription of the tribe and its genera recognized closely follows that of Webster (1975, 1994) in his classification of the Euphorbiaceae. Two exceptions are recognition of the genera *Tragiella* Pax & K. Hoffm. (following Radcliffe-Smith, 1982, 1987) and *Pachystylidium* Pax & K. Hoffm. (following Airy Shaw, 1969, 1975), both originally described as species of *Tragia*. In addition, several taxonomic and nomenclatural changes have taken place since Webster's 1975 synopsis. The monotypic genera *Vigia* Vellozo (which has priority over the more commonly used generic name *Fragariopsis* A. St. Hil.) and *Eleutherostigma* Pax & K. Hoffm. have been synonymized under *Plukenetia* (Gillespie, 1993). Adrien Jussieu's genus *Anabaena* has been twice renamed, as *Romanoa* by Trevisan (1848) and as *Anabaenella* by Pax & Hoffmann (1919), due to similarity with its namesake cyanobacteria. Although the cyanobacteria were originally described as *Anabaina* Bory, the more commonly used name of *Anabaena* Bory was recently conserved against *Anabaena* Adr. Juss. (ICBN, Greuter, 1988: 112). *Romanoa*, the name rediscovered by Punt (1962) and Radcliffe-Smith (1980), thus becomes the valid name for the genus.

The most recent monograph of the Plukenetieae (as subtribe Plukenetiinae of tribe Acalypheae) was by Pax & Hoffmann (1919; with additions and changes, 1924, 1931). The authors treated a number of segregate genera in addition to *Tragiella* and *Pachystylidium* that were not recognized by Webster (1975); these are *Gitara* Pax & K. Hoffm., considered synonymous with *Acidoton* Sw. (Webster, 1967), and *Tetracarpidium* Pax (also known as *Angostylidium* (Muell. Arg.) Pax & K. Hoffm.), *Apodandra* Pax & K. Hoffm. and *Pterococcus* Hassk., all presently treated under *Plukenetia* L. (Gillespie, 1993). A second difference is Webster's recognition of *Megistostigma* Hook. f. following

Croizat (1941) and Airy Shaw (1969); of the two species treated by Pax and Hoffmann, *M. malaccense* Hook. f. was considered a species of *Sphaerostylis* Baill. and *M. peltatum* (J. J. Sm.) Croizat as the monotypic *Clavistylus* J. J. Sm. The genus *Ramelia* Baill. has since been reduced to synonymy under *Bocquillonia* Baill. (Acalyphoideae, tribe Alchornieae) and thus excluded from the Plukenetieae (Airy Shaw, 1968, 1974), while *Megalostylis* is now considered to be a synonym of *Dalechampia* (Webster & Armbruster, 1991).

In his most recent classification, Webster (1994) treats *Dalechampia* as a subtribe, the Dalechampiinae, of the Plukenetieae, rather than as a distinct but related tribe (as in Webster, 1975). Although the genus will not be extensively treated in the present paper, its pollen morphology will be discussed in relation to the Plukenetieae.

In the first attempt at an infratribal classification and consideration of relationships, Pax & Hoffmann (1919) divided the 19 genera of their "Plukenetiinae" into four informal groups, Plukenetiiformes, Astrococciformes, Tragiiformes, and Sphaerostyliformes, based primarily on stamen number and style shape. Webster (1975) created the first formal subtribal classification upon describing the Tragiinae. The Tragiinae are characterized by presence of stinging hairs, a trilocular ovary, and absence of foliar glands; species are found in all habitats but are particularly diverse in dry areas. In contrast, the Plukenetiinae are characterized by absence of stinging hairs, foliar glands typically present and an ovary that is usually 4-locular or less often trilocular, and are usually found in wet habitats. Style morphology has been used extensively in infratribal classification and generic delimitation. With the exception of the genus *Tragia*, there has been an unusual radiation in style morphology in the Plukenetieae. Within subtribe Tragiinae, many of the genera are characterized and differentiated from *Tragia* on the basis of unusually shaped massive styles (e.g., *Sphaerostylis*, *Megistostigma*, *Cnesmone* Blume, and *Tragiella*). Pax & Hoffmann (1919, 1931) based their sectional classification of *Plukenetia* on style morphology.

Since *Tragia* is a large and diverse genus it is necessary to consider an infrageneric classification. Eight sections are recognized in the present study. The sectional classification of Pax & Hoffmann (1919, 1931) is followed with the following exceptions. Section *Leptobotrys* (Baill.) Muell. Arg. is considered distinct from section *Tragia*, whereas sections *Leucandra* (Klotzsch) Muell. Arg. and *Ratiga* Muell. Arg. are treated as part of section

Tragia (following Miller & Webster, 1967, and Múlgura de Romero & Gutiérrez de Sanguinetti, 1989). Also considered is Léandri's subgenus *Mauroya*, which includes a single Madagascan species. Many of the sections have in the past been recognized as distinct genera (e.g., *Bia* Klotzsch, *Ctenomeria* Harv., *Lassia* Baill., *Leptobotrys* Baill., *Leucandra* Klotzsch, and *Zuckertia* Baill.).

Previous pollen morphological studies of the Plukenetieae have been based only on LM (Erdtman, 1952; Punt, 1962; Miller & Webster, 1967), with the exception of studies dealing only briefly with pollen morphology (e.g., Gillespie, 1988; Múlgura de Romero & Gutiérrez de Sanguinetti, 1989). The most extensive survey was that of Punt (1962), who examined 17 genera (equivalent to 12 in the classification followed here) in his pollen survey of the Euphorbiaceae. Pollen types within the tribe fell into two of Punt's 17 main groups, the *Plukenetia* configuration and the *Cnesmosa* (= *Cnesmone*) configuration. The *Plukenetia* configuration is characterized by oblate-spheroidal to oblate, tricolpate or triporate grains with broad apertures having a "ruptured membrane." Of the two types within this main group, the *Plukenetia* type is tricolpate and includes all examined species of the Plukenetiinae, African *Tragiinae*, and most New World *Tragia* spp. The *Pachystylidium* type is triporate and includes only that genus. The *Cnesmosa* configuration is characterized as inaperturate and lacking a crotonoid exine; three of its five types are composed of species of the Plukenetieae. The *Cnesmosa* type of pollen with a psilate exine includes *Acidoton*, *Megistostigma*, and *Cnesmone*. The *Tragia fallax* type of pollen is described as having an "intectate pilate exine" and consists of *Tragia* sect. *Bia* (Klotzsch) Muell. Arg. The *Platygyne* (= *Platygyne*) type of pollen with an exine that is tectate and "intra-reticulate" (defined by Punt as "columellae inside the tectum form[ing] a network") consists only of species of *Platygyne* Mercier. Punt concluded that pollen morphology supported the distinctness of *Tragia* sect. *Bia*, the close relationship of *Haematostemon* (Muell. Arg.) Pax & K. Hoffm., *Angostyles* Benth., and *Astrococcus* Benth., and the observation that *Apodandra*, *Romanoa*, *Fragariopsis* (= *Vigia*), *Pterococcus*, and *Angostylidium* cannot be easily distinguished from *Plukenetia*. Pollen evidence also supported Croizat's (1941) circumscription of *Sphaerostylis* and *Megistostigma*. Miller & Webster (1967) examined pollen of *Tragia* species from the United States; evidence from their study of pollen and floral morphology led them to revive section *Leptobotrys* (Baill.) Muell. Arg., which was

considered part of section *Tragia* by Pax & Hoffmann (1919), and to doubt the taxonomic validity of section *Leucandra* (Klotzsch) Muell. Arg.

METHODS

Flowers were removed from herbarium specimens, of which determinations were verified, and rehydrated in 3% Aerosol-OT for 3–4 days. Pollen grains were isolated and mounted in Hoyer's medium (Radford et al., 1974) for examination under LM. The method of Lynch & Webster (1975) was followed for SEM studies. Pollen grains were dehydrated to 100% ethanol, to 100% amyl acetate, and then critical-point dried. Following sputter coating with gold or a gold/palladium mixture, grains were examined and photographed in an ISI DS130 (equipped with a LaB₆ filament), Hitachi S800, or Cambridge 250 scanning electron microscope. All pollen was prepared in the above manner unless specified otherwise. In several cases pollen was acetolyzed (following the method of Erdtman, 1952) then mounted directly on a stub and sputter coated for examination under SEM. Voucher microscope slides and electron micrographs are deposited at the Systematics Laboratory, Botany Department, University of California, Davis. Voucher LM slides of acetolyzed pollen are deposited at the Palynology Laboratory, Botany Department, Smithsonian Institution, Washington, D.C.

Descriptions of pollen grains are based on observations under LM and SEM. Measurements were made under LM on 15 grains mounted in Hoyer's medium. The polar axis (P), equatorial axis (E), and the polar to equatorial axis ratio (P/E) are given in the generic descriptions as the range of mean values of collections examined (refer to Table 1 for measurements of individual collections). In the case of inaperturate grains that are ellipsoidal in shape, the shortest axis (S) and longest axis (L) are given. Exine thickness of aperturate grains was measured at mid mesocolpium in polar view. Terminology used follows that of Erdtman (1952, 1966) and Walker & Doyle (1975). In the present paper the term scabrate is restricted to the description of a surface having a covering of microprojections that are irregular in size, shape, and distribution (e.g., Figs. 27, 48, 69). The term microverrucae (e.g., Figs. 9, 38, 41, 43) is introduced to refer to microprojections that are more regular in size, wider than high, and rounded in shape but not constricted at the base (as distinguished from conical spinules and constricted-based microgemmae).

Twelve of the 13 genera in the Plukenetieae

TABLE 1. Species of Plukenetieae examined with voucher information, geographical location, pollen size dimensions (minimum–maximum (mean)) of polar axis (P Axis) and equatorial axis (E Axis), all in μm , and pollen shape given as ratio of polar to equatorial axes (P/E). Inaperturate pollen is indicated by an asterisk; shortest axis (under P Axis) and longest axis (under E Axis) are given if pollen shape is ellipsoid, otherwise a single diameter is given if spheroidal. Pollen with apertures not easily visible under LM is indicated by a “c”; shortest and longest axes are given. Measurements of acetolyzed pollen are preceded by an “a.”

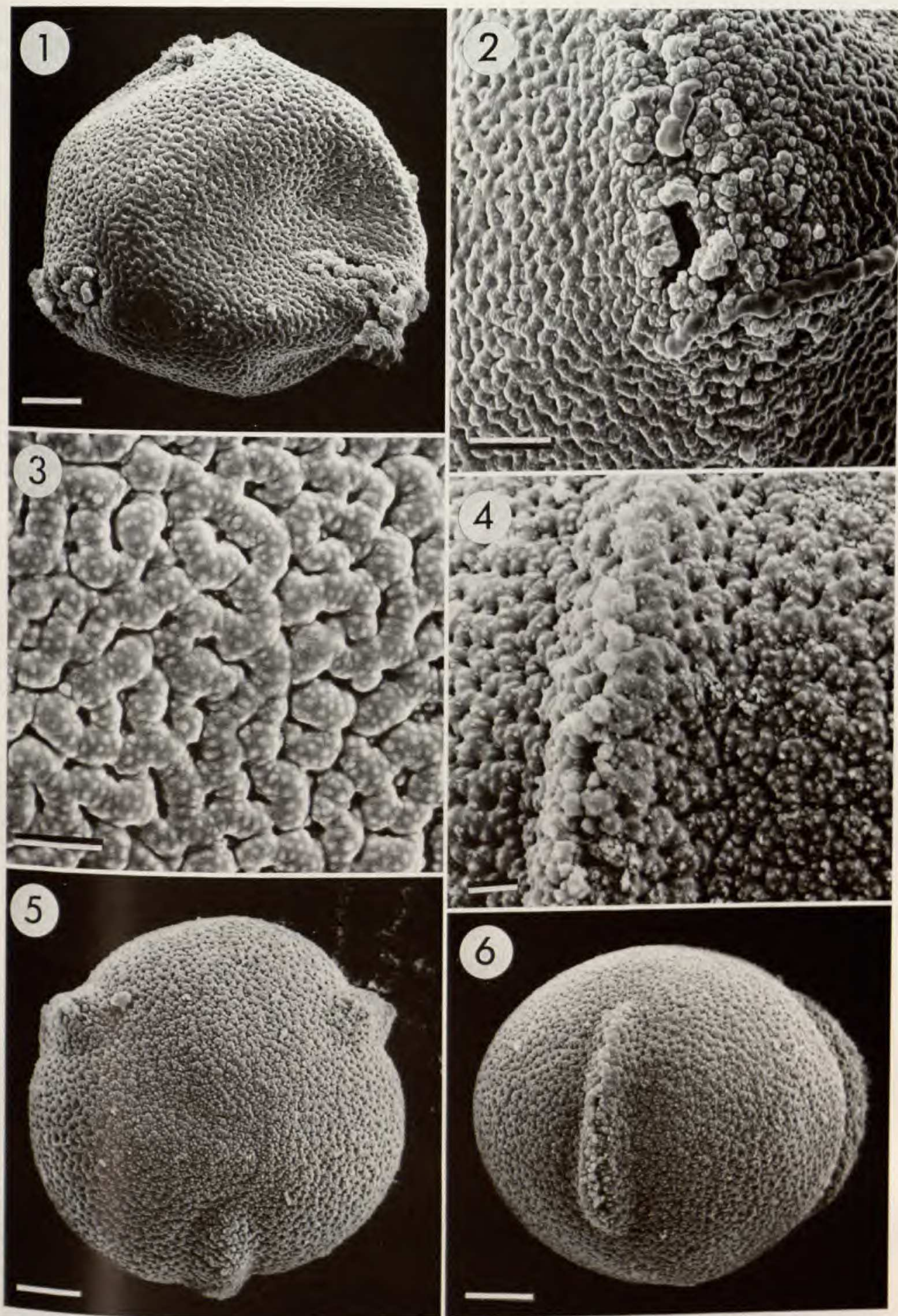
Species	Collection	Location	P Axis	E Axis	P/E
Plukenetiinae					
<i>Angostyles longifolia</i> Benth.	Spruce 2282, NY	Brazil	52–60 (54)	58.5–67.5 (62)	0.87
<i>Astrococcus cornutus</i> Benth.	Liesner 8693, NY	Venezuela	43.5–52 (48)	50.5–57.5 (54.5)	0.88
<i>A. cornutus</i> Benth.	Liesner 8693, NY	Venezuela	a 34.5–41.5 (37.5)	41.5 48.5 (46)	0.82
<i>Eleutherostigma lehmannianum</i> Pax & K. Hoffm.	Cazalet & Pennington 5089, UC	Ecuador	48.3–53 (50.5)	53–60 (56.5)	0.89
<i>Haematostemon coriaceus</i> (Baill.) Pax & K. Hoffm.	Wurdack & Adderley 43210, NY	Venezuela	33.5–37 (35)	38–43.5 (40.5)	0.86
<i>H. guianensis</i> Sandw.	Fanshawe 2869, US	Guyana	41.5–46 (44)	47–50.5 (49.5)	0.89
<i>Plukenetia africana</i> Sond.	Pope et al. 834, MO	Botswana	34–39 (36.5)	43–49.5 (45.5)	0.80
<i>P. africana</i> Sond.	Wild 5062, MO	Botswana	34–40.5 (36.5)	40.5–48 (44)	0.83
<i>P. brachybotrya</i> Muell. Arg.	Vargas 18799, US	Peru	49.5–57 (53)	60–67.5 (62)	0.85
<i>P. conophora</i> Muell. Arg.	Zenker 3394, US	Cameroon	34–37.5 (35)	41.5–45.5 (42.5)	0.82
<i>P. conophora</i> Muell. Arg.	Zenker 3394, US	Cameroon	a 27.7–32 (30.5)	32–41.5 (36.5)	0.84
<i>P. corniculata</i> Smith	Koorders 41720, UC	Indonesia	34.5–37 (35)	41.5–46 (43.5)	0.80
<i>P. loretensis</i> Ule	Fosberg 29094, MO	Peru	50.5–62 (55)	60–76 (66.5)	0.83
<i>P. loretensis</i> Ule	Maguire & Politi 27371, US	Venezuela	48.5–57.5 (53)	57.5–69 (64)	0.83
<i>P. penninervia</i> Muell. Arg.	Werff & Wingfield 3173, DAV	Venezuela	30–39 (34)	39–48 (43)	0.79
<i>P. penninervia</i> Muell. Arg.	Standley 56708, A	Honduras	35–43 (37.5)	45.5–52 (48)	0.79
<i>P. polyadenia</i> Muell. Arg.	Lindeman 6134, DAV	Surinam	50.5–60 (56)	57.5–69 (63)	0.89
<i>P. madagascariensis</i> Léandri	Morat 4893, P	Madagascar	37.5–40.5 (39)	43–46 (45.5)	0.86
<i>P. multiglandulosa</i> Jabl.	Cowan & Wurdack 31400, US	Venezuela	32.5–37.5 (35)	40.5–47 (43.5)	0.80
<i>P. stipellata</i> L. J. Gillespie	Gillespie 418, DAV	Costa Rica	53–60 (56)	57.5–69 (64.5)	0.87
<i>P. supraglandulosa</i> L. J. Gillespie	Cowan 38204, US	French Guiana	31–33 (32)	39–45 (41)	0.78
<i>P. verrucosa</i> Smith	Prance et al. 11255, DAV	Brazil	34.5–39 (37)	42.5–50.5 (46.5)	0.80
<i>P. volubilis</i> L.	Asplund 14129, US	Peru	49.5–58.5 (53)	58.5–65 (62)	0.85

TABLE 1. Continued.

Species	Collection	Location	P Axis	E Axis	P/E
<i>Romanoa tamnoides</i> (Adr. Juss.) A. Radcliffe-Smith	Webster et al. 25436, DAV	Brazil	53-55 (54.5)	58.5-62 (60)	0.91
<i>Vigia serrata</i> Vell.	Bradem et al. 8376, DAV	Brazil	36.5-46 (38.5)	46-55 (49)	0.79
<i>V. serrata</i> Vell.	Hoehne 29250, A	Brazil	ca. 32-35	ca. 42-51	
Tragiinae					
<i>Acidoton nicaraguensis</i> (Hemsley) Webster	Ortiz 1104, DAV	Nicaragua	34.5-39 (37)	39-46 (42)	0.88
<i>A. nicaraguensis</i> (Hemsley) Webster	Steyermark & Davidse 116239, DAV	Venezuela	39-41.5 (40)	39-48 (44)	0.91
<i>A. urens</i> Swartz	Proctor 36826, MO	Jamaica	* 37-46 (41.5)	39-48 (44)	—
<i>A. microphyllus</i> Urb.	Leonard 5248, US	Haiti	* 34-40.5 (37.5)	35-45.5 (40.5)	—
<i>Cnesmone anisosepala</i> (Merr. & Chun) Croiz.	Lau 141, UC	China	c 52-57.5 (55)	52-60 (56)	—
<i>C. javanica</i> Blume	Morse 567, NY	China	c 45.4-50.5 (47.5)	47-52 (49.5)	—
<i>C. philippinensis</i> (Merr.) Airy Shaw	Ramos & Edaño 47087, UC	Philippines	c 48.5-55 (52)	50.5-57.5 (54.5)	—
<i>C. tonkinensis</i> (Gagnep.) Croiz.	Pételot 6521, A	Vietnam	c 46-49.5 (47.5)	48.5-53 (51)	—
<i>Megistostigma cordata</i> Merr.	Ramos 17591, US	Philippines	c 48-58.5 (51)	48-58.5 (53)	—
<i>M. malaccense</i> Hook. f.	Rahmat si Toroes 1389, A	Indonesia	* 46-53 (48.5)	48.5-57.5 (52)	—
<i>M. malaccense</i> Hook. f.	Burkhill & Haniff 15589, MO	Malaysia	* 42.5-53 (48)	46-57.5 (52)	—
<i>Pachystylidium hirsutum</i> (Blume) Pax & K. Hoffm.	Clemens 1748, UC	Philippines	27.5-32 (30.5)	30-35.5 (33)	0.92
<i>P. hirsutum</i> (Blume) Pax & K. Hoffm.	Ramos & Edaño 49201, UC	Philippines	31-33.5 (32)	34.5-39 (36.5)	0.88
<i>Platygynea hexandra</i> (Jacq.) Muell. Arg.	Howard et al. 81, A	Cuba	* —	37-44 (40)	—
<i>P. hexandra</i> (Jacq.) Muell. Arg.	Jack 7146, US	Cuba	* 35-41.5 (38.5)	37.5-44 (41)	—
<i>P. leonis</i> Alain	Léon 12176, DAV	Cuba	* 30-32 (32)	30-34.5 (32.5)	—
<i>P. parvifolia</i> Alain	Schafer 1427, NY	Cuba	* 30-39 (34.5)	35-40 (38.5)	—
<i>Tragia adenanthera</i> Baill.	Tanner 672, UC	Tanzania	31-39 (34.5)	34.5-46 (39)	0.88
<i>T. bailloniana</i> Muell. Arg.	Cowan 2692, DAV	Mexico	53-57.7 (56)	60-66.5 (62.5)	0.90

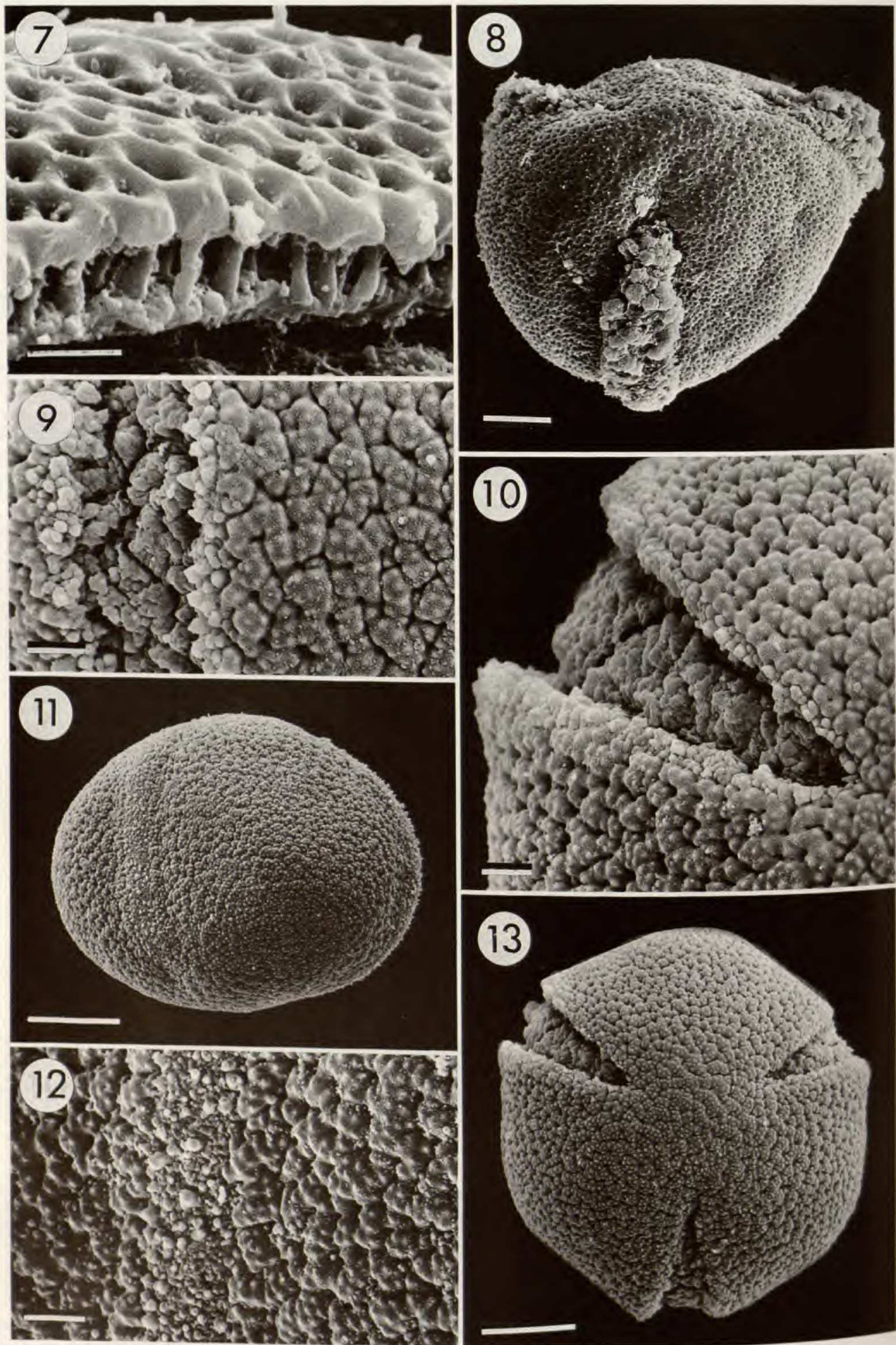
TABLE 1. Continued.

Species	Collection	Location		P Axis	E Axis	P/E
<i>T. capensis</i> Thunb.	<i>Ecklon & Zeyher s.n.</i> , US 1170932	South Africa		27.5–32 (31)	30–37 (35)	0.89
<i>T. capensis</i> Thunb.	<i>Kuntze s.n.</i> , NY	South Africa	a	23–30 (26)	27.5–33.5 (29.5)	0.88
<i>T. chlorocaulon</i> Baill.	<i>Eiten & Eiten</i> 4285, US	Brazil		30–35 (32.5)	34–43 (38.1)	0.85
<i>T. cordifolia</i> Vahl	<i>Webster s.n.</i> , DAV	Kenya		30–37 (34)	37–43.5 (39)	0.88
<i>T. hispida</i> Willd.	<i>Nicolson</i> 2991, US	India		36.5–40.5 (38)	41.5–45.5 (43.5)	0.87
<i>T. involucrata</i> L.	<i>Nicolson et al.</i> HFP173, US	India		30–34 (31.5)	34–40 (36)	0.87
<i>T. ivohibeensis</i> Leandri	<i>Humbert</i> 3387, DAV	Madagascar		41.5–46 (43.5)	44–55 (48)	0.91
<i>T. lessertiana</i> (Baill.) Muell. Arg.	<i>Webster</i> 24119, DAV	Surinam	*	—	46–53 (49)	—
<i>T. mexicana</i> Muell. Arg.	<i>Tuerckheim</i> 7664, US	Guatemala		30–35 (33)	35–40.5 (38)	0.87
<i>T. novae-hollandiae</i> Muell. Arg.	<i>Dovey</i> B56, UC	Australia		33.5–38 (36)	39–45 (41)	0.88
<i>T. pacifica</i> McVaugh	<i>McVaugh</i> 21006, DAV	Mexico		27.5–32 (30)	33.5–38 (35.5)	0.85
<i>T. peltata</i> Klotzsch	<i>dos Santos</i> 1551, DAV	Brazil		24–26.5 (25)	27.5–34.5 (30)	0.83
<i>T. polyandra</i> Vell.	<i>Bresolin</i> 629, US	Brazil		31–36.5 (33.5)	36.5–31.5 (38.5)	0.87
<i>T. ramosa</i> Torr.	<i>Ferris & Bacigalupui</i> 8136, DAV	U.S.A.		25.5–32 (28)	30–37 (32)	0.88
<i>T. scandens</i> (Baill.) Muell. Arg.	<i>Humbert</i> 13741, P	Madagascar		31–37.5 (33)	34–41.5 (38.5)	0.86
<i>T. sellowiana</i> (Klotzsch) Muell. Arg.	<i>Webster</i> 25463, DAV	Brazil	*	—	48.5–57.5 (54)	—
<i>T. smallii</i> Shinnars	<i>Curtiss s.n.</i> , US	U.S.A.		35–39 (37)	37.5–44 (40.5)	0.92
<i>T. tristis</i> Muell. Arg.	<i>Anderson</i> 9117, DAV	Brazil		32–41.5 (37)	39–48 (43.5)	0.85
<i>T. urens</i> Small	<i>Norris</i> 759, DAV	U.S.A.		32–37 (34)	34.5–43.5 (38)	0.89
<i>T. volubilis</i> L.	<i>Webster & Proctor</i> 5325, DAV	Jamaica		25.5–27.5 (27)	30–33.5 (31)	0.87
<i>Tragiella natalensis</i> (Sond.) Pax & K. Hoffm.	<i>Mearns</i> 295, NY	Kenya		39–46 (42.5)	43.5–50.5 (46.5)	0.91
<i>T. natalensis</i> (Sond.) Pax & K. Hoffm.	<i>Mearns</i> 295, NY	Kenya	a	33.5–39 (36.5)	38–43 (39.5)	0.92



FIGURES 1-6.^a Scanning electron micrographs of pollen of *Angostyles* and *Astrocooccus* (subtribe Plukenetiinae). 1-3. *Angostyles longifolia*.—1. Polar view.—2. Close-up of colpus.—3. Exine sculpture. 4-6. *Astrocooccus cornutus*.—4. Close-up of colpus.—5. Polar view.—6. Equatorial view. Scale bar: = 10 μ m in Figs. 1, 5, 6; = 5 μ m in Fig. 2; = 2 μ m in Figs. 3, 4.

^a Voucher information is in Table 1 unless given in the caption.



FIGURES 7-13.³ Scanning electron micrographs of pollen of *Eleutherostigma* and *Haematostemon* (subtribe Plukenetiiinae). 7-8. *Eleutherostigma lehmannianum*.—7. Exine structure of mesocolpium of fragmented grain.—8. Oblique view. 9-13. *Haematostemon coriaceus*.—9. Close-up of colpus in equatorial view lacking a continuous

and a total of 55 species were examined (Table 1). Pollen of *Sphaerostylis*, a small genus of vines endemic to Madagascar, and one section of *Tragia* endemic to Madagascar, *Agirta* Baill., was not available.

RESULTS—SUBTRIBE PLUKENETIINAE

Angostyles (Figs. 1–3). A monotypic genus of small trees known only from the Rio Negro region of Amazonian Brazil.

Pollen suboblate ($P/E = 0.87$), $54\ \mu\text{m}\ P \times 62\ \mu\text{m}\ E$, tricolpate; amb subcircular to obscurely obtuse-triangular; colpus narrow and short, margins uneven; exine tectate-perforate, $1\text{--}1.5\ \mu\text{m}$ thick, uniformly thickened; tectum very finely foveolate-rugulate, fragmented and irregularly finely gemmate at colpus margin, rugae with evenly spaced microverrucae, intervening perforations narrow, sinuous to sometimes small and circular.

Astrococcus (Figs. 4–6). A monotypic genus of shrubs or small trees in the upper Rio Negro region of Venezuela and Brazil.

Pollen suboblate to oblate-spheroidal ($P/E = 0.88$), $48\ \mu\text{m}\ P \times 54.5\ \mu\text{m}\ E$, tricolpate; amb subcircular to obscurely obtuse-triangular; colpus very narrow and short, sometimes covered with an unbroken sexinous membrane, margins uneven; exine tectate-perforate, $1.5\text{--}2\ \mu\text{m}$ thick, becoming thicker, ca. $2.5\text{--}3\ \mu\text{m}$, and distinctly raised at colpus margin, with upper and lower exine layers separating forming an elongate chamber in the vicinity of the colpus; tectum very finely foveolate-rugulate, fragmented and irregularly, finely gemmate at colpus margin, rugae with $2\text{--}(3)$ rows of evenly spaced microverrucae, intervening perforations very narrow, sinuous to small and circular particularly near the colpus.

A continuous unbroken sexine may sometimes be present over the apertures as in pollen of *Haematostemon* (Figs. 11, 12; refer to description and discussion under *Haematostemon*).

Eleutherostigma (= *Plukenetia*) (Figs. 7, 8). A monotypic genus of lianas of premontane forest in Colombia and Ecuador, its single species now treated as a species of *Plukenetia*, *P. lehmanniana* (Pax & K. Hoffm.) Huft & L. J. Gillespie.

Pollen oblate-spheroidal ($P/E = 0.89$), $50.5\ \mu\text{m}\ P \times 56.5\ \mu\text{m}\ E$, tricolpate; amb obtuse-triangular,

angulaperturate; colpus broad with ends often indistinct, margins uneven and jagged; exine tectate-perforate, $2\text{--}2.5\ \mu\text{m}$ thick, somewhat thinner at colpus margin; tectum foveolate, surface smooth.

Haematostemon (Figs. 7–13). Two species of shrubs or small trees in Guyana and Amazonas, Venezuela, both examined.

Pollen suboblate to oblate-spheroidal ($P/E = 0.86\text{--}0.89$), $35\text{--}44\ \mu\text{m}\ P \times 40.5\text{--}49.5\ \mu\text{m}\ E$, tricolpate; amb subcircular; colpus narrow, sometimes covered with an unbroken sexinous membrane, margins uneven; exine tectate-perforate, $1.5\text{--}2\ \mu\text{m}$ thick, becoming thicker, $3\text{--}3.5\ \mu\text{m}$, at colpus margin, with upper and lower exine layers separating forming an elongate chamber in the vicinity of the colpus; tectum very finely foveolate-rugulate, becoming fragmented and irregularly gemmate at colpus margin, rugae with $(1\text{--})2\text{--}(3)$ rows of evenly spaced microverrucae, intervening perforations narrow, sinuous to small and circular; apertural sexine, when present, densely and irregularly scabrate.

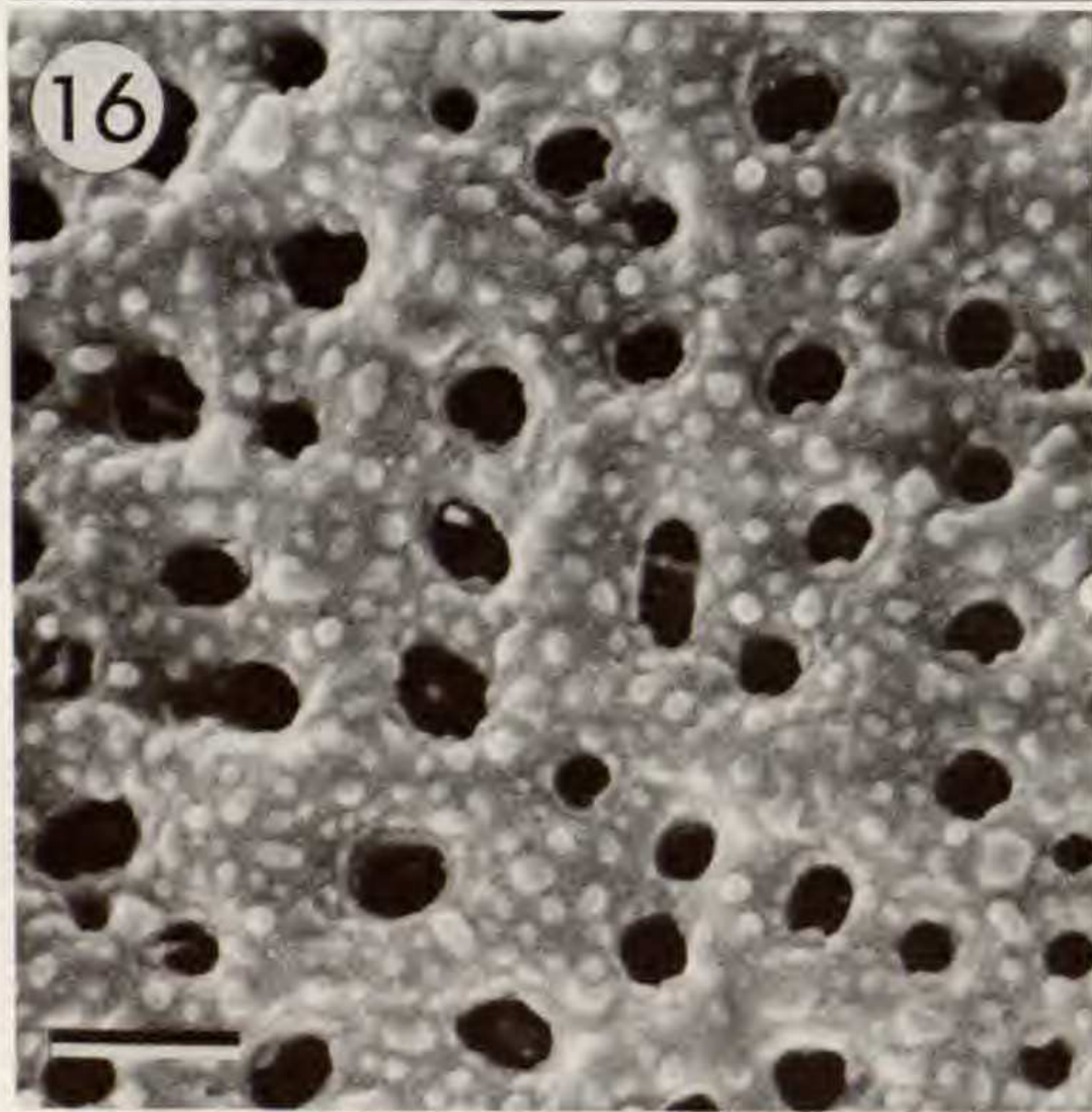
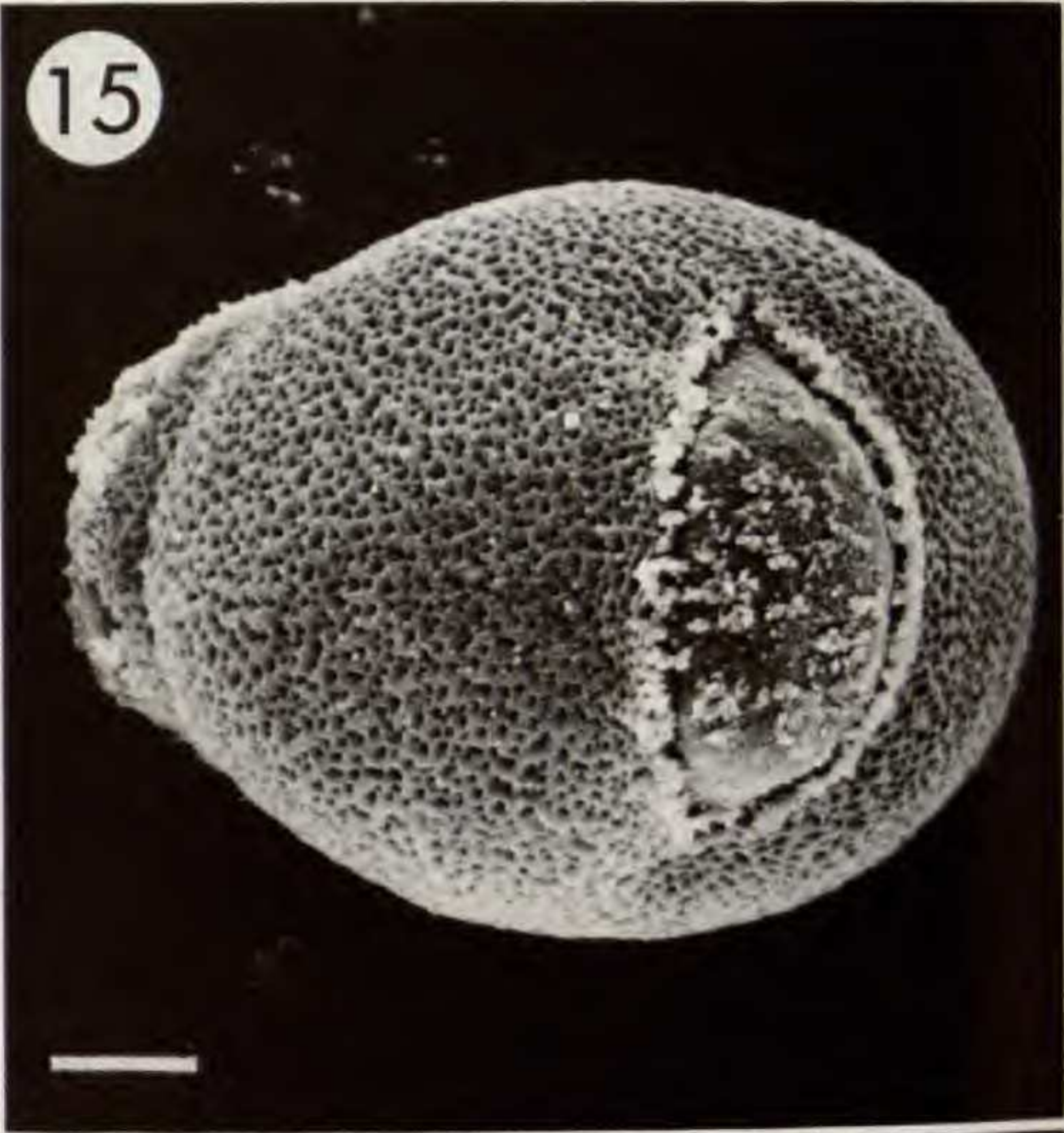
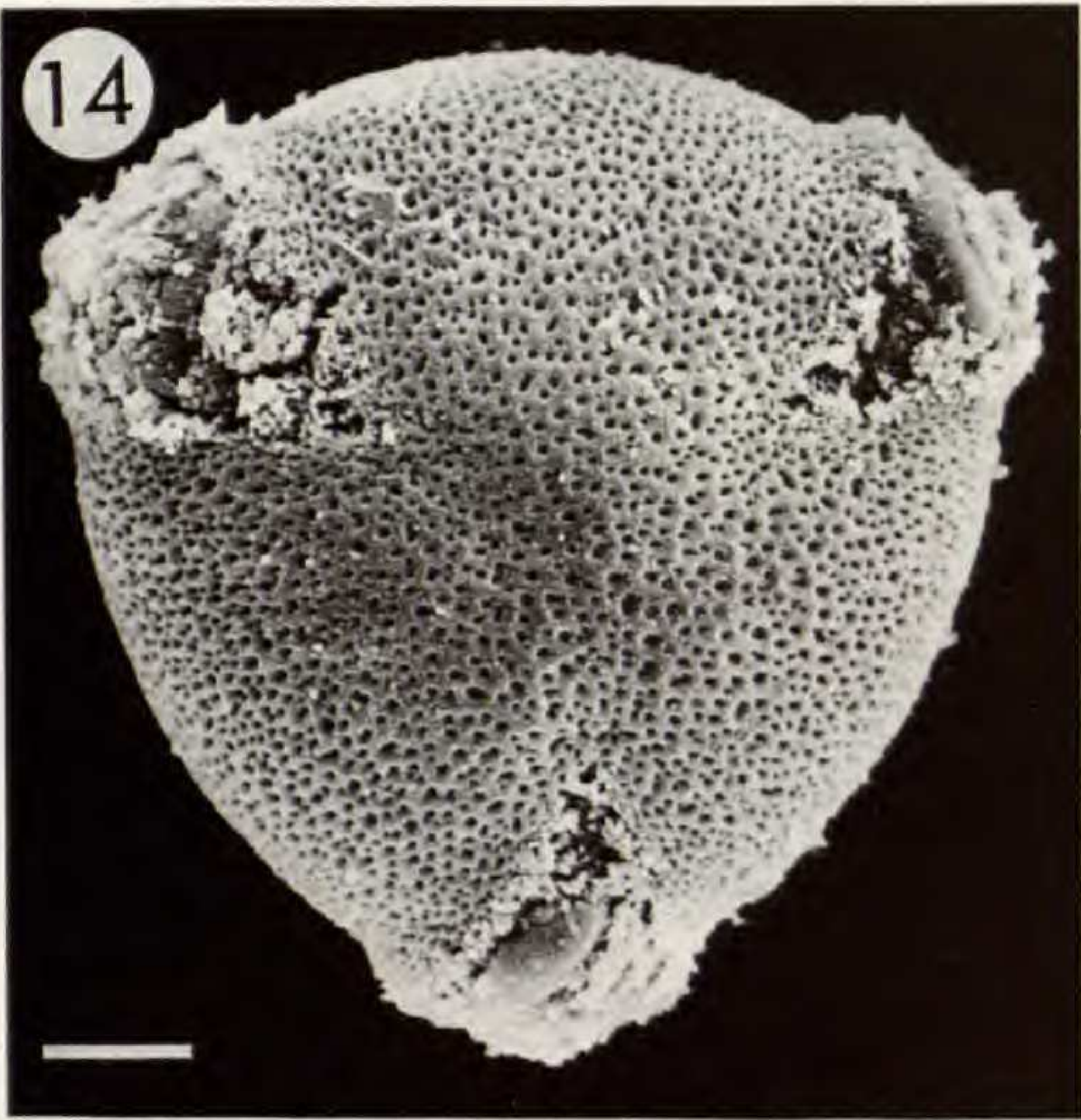
Grains within a single SEM preparation have apertures that appear to have a sexine that is continuous (Figs. 9, 10) or very fragmented (or sometimes absent) (Figs. 7, 8, 11, 12) over the apertures. This difference may perhaps be due to degree of rehydration or tolerance to treatment with acetone or sonication, resulting in some grains having a ruptured or degraded apertural sexine.

Plukenetia (Figs. 14–24). A genus of 16 species of twining vines and lianas distributed pantropically with one species in Asia, four in Africa and Madagascar, and 11 in the Neotropics (note that the two species previously treated as species of *Eleutherostigma* and *Vigia* are included in the species count but are described separately). The 13 species examined may be divided into two pollen types based on tectum morphology.

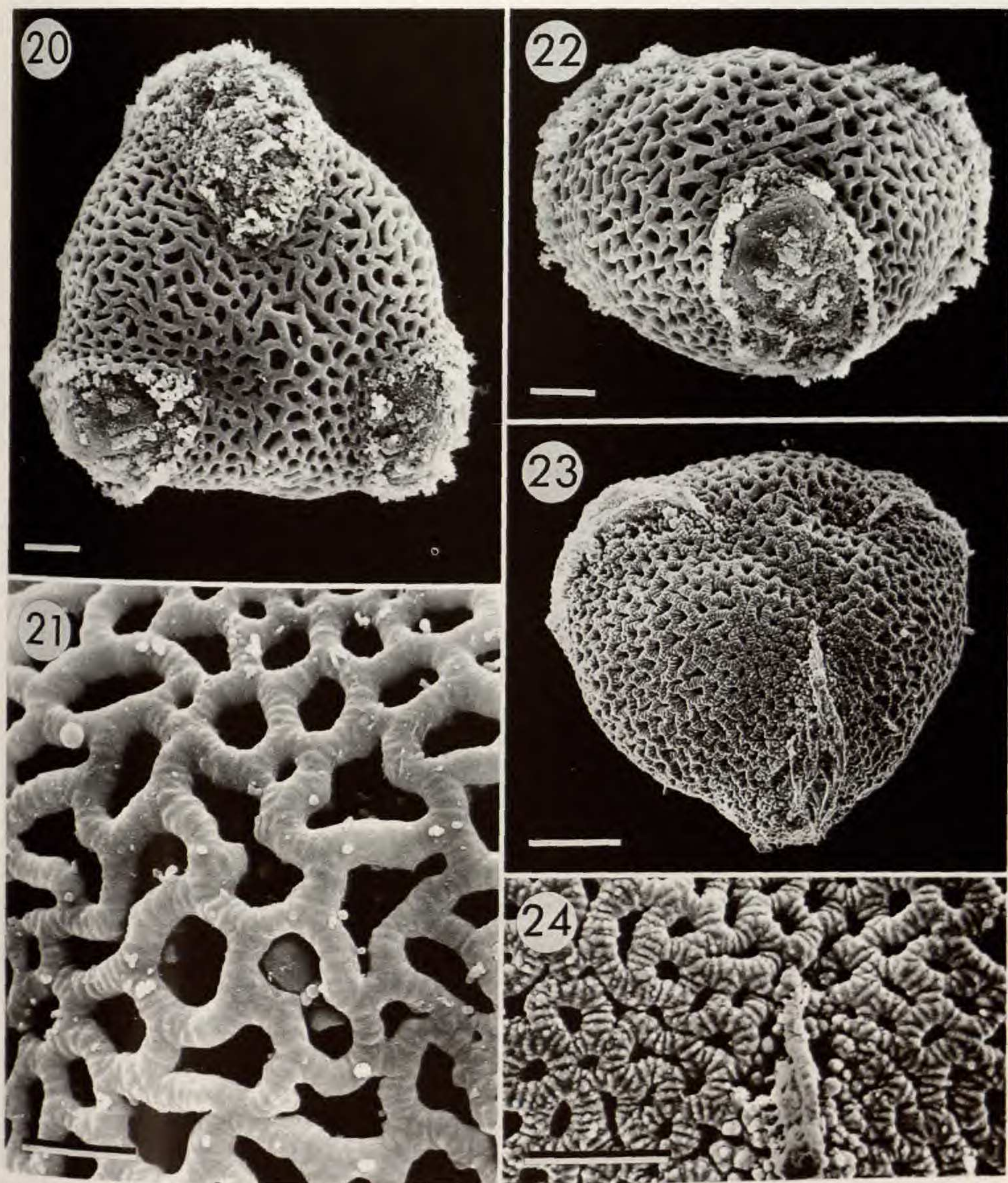
Type 1 (Figs. 14–19). Pollen suboblate to oblate-spheroidal ($P/E = 0.80\text{--}0.89$), $35\text{--}56\ \mu\text{m}\ P \times 42.5\text{--}64.5\ \mu\text{m}\ E$, tricolpate; amb obtuse-triangular to subcircular, angulaperturate; colpus broad with margins very uneven and jagged; exine tectate-perforate, $1.5\text{--}4\ \mu\text{m}$ thick; tectum foveolate with foveolae sometimes becoming smaller at aperture margin, surface smooth or scabrate (e.g., *P. stipellata*).

Of the seven species included in Type 1, the

apertural sexine.—10. Close-up of colpus of grain in Fig. 13; note lack of an apertural sexine.—11. Equatorial view.—12. Close-up of colpus of grain in Fig. 11; note presence of sexine covering aperture.—13. Polar view of grain lacking a distinct apertural sexine. Scale bar: = $10\ \mu\text{m}$ in Figs. 8, 11, 13; = $2\ \mu\text{m}$ in Figs. 7, 9, 10, 12.



FIGURES 14-19.³ Scanning electron micrographs of pollen of *Plukenetia* (pollen Type 1). 14-16. *P. stipellata*.—14. Polar view.—15. Equatorial view.—16. Exine sculpture.—17. Polar view of *P. polyadenia*.—18. Polar view of *P. africana* (Wild 5062 MO).—19. Equatorial view of acetolyzed grain of *P. conophora*. Scale bar: = 10 μm in Figs. 14, 15, 17-19; = 2 μm in Fig. 16.

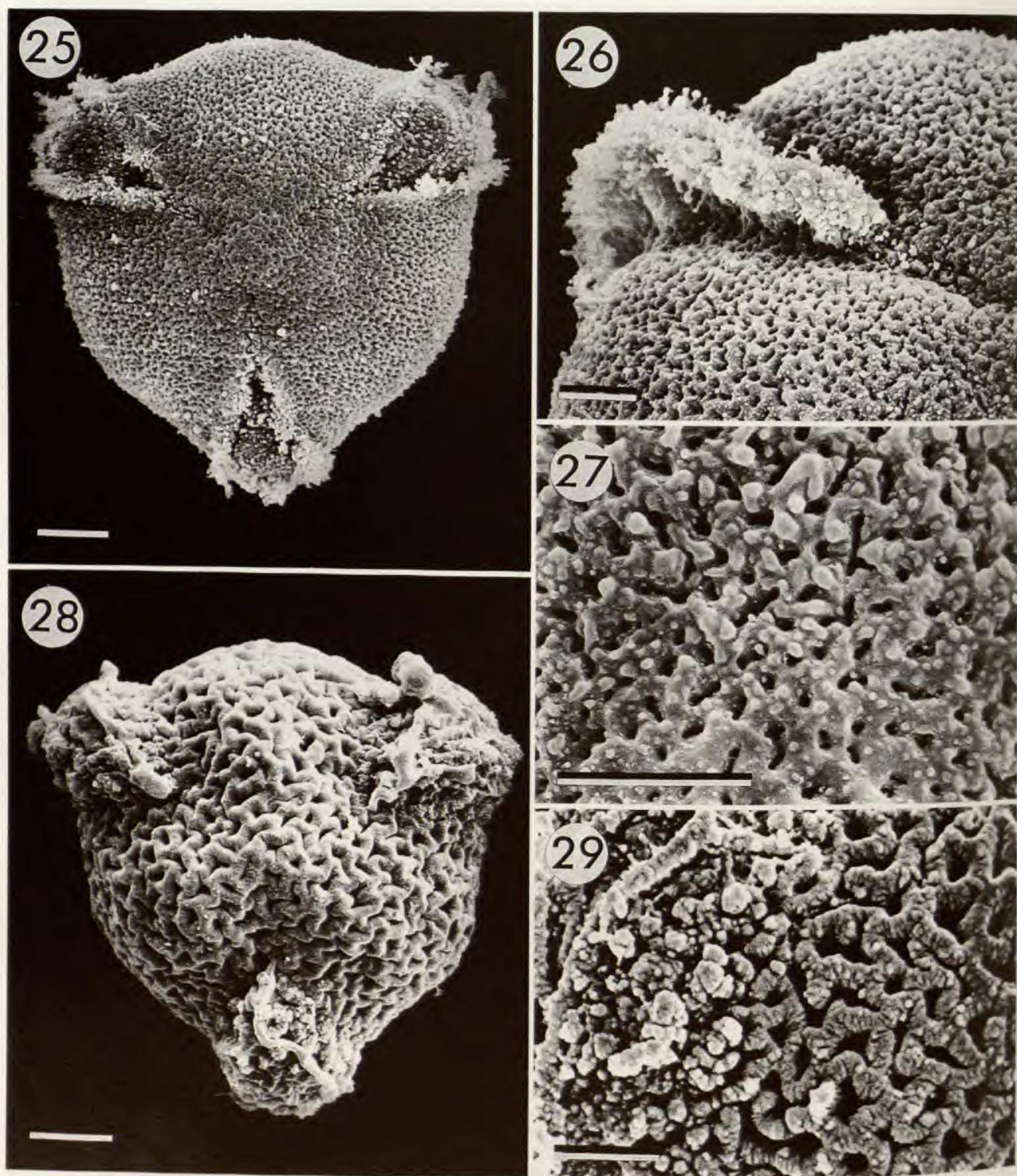


FIGURES 20–24.¹ Scanning electron micrographs of pollen of *Plukenetia* (pollen Type 2). 20–22. *P. loretensis* (Maguire & Politi 27371 US). —20. Polar view. —21. Exine sculpture. —22. Equatorial view. 23–24. *P. penninervia* (Standley 56708 A). —23. Oblique view. —24. Close-up of colpus and exine sculpture. Scale bar: = 10 μm in Figs. 20, 22, 23; = 5 μm in Figs. 21, 24.

New World species, *Plukenetia polyadenia* (Fig. 17), *P. stipellata* (Figs. 14–16), and *P. volubilis* have large pollen grains (57–69 μm E) with an amb usually obtuse-triangular and an exine 2–4 μm thick that becomes gradually thinner at the colpus margin. The Old World species, *P. africana* (Fig. 18), *P. conophora* (Fig. 19), *P. corniculata*, and *P. madagascariensis* have medium-sized pollen grains (41–50 μm E) with a subcircular amb and an exine 1.5–2.5 μm that is mostly uniformly thick or sometimes thickened at the colpus margin.

Type 2 (Figs. 20–24). Pollen suboblate ($P/E = 0.78\text{--}0.85$), 32–55 μm $P \times 41\text{--}66.5$ μm E , tricolpate; amb obtuse-triangular, angulaperturate; colpus broad with margins very uneven and jagged; exine semitectate-reticulate, 2.5–4.5 μm thick; muri usually crenate (i.e., transversely ridged), becoming fragmented and sometimes finely gemmate at colpus margin, lumina often smaller near colpus margin.

Of the six species included in Type 2, *Plukenetia brachybotrya* and *P. loretensis* (Figs. 20–22) have



FIGURES 25–29.³ Scanning electron micrographs of pollen of *Romanoa* and *Vigia* (subtribe Plukenetinae). 25–27. *Romanoa tamnoides*.—25. Polar view.—26. Close-up of colpus of grain less expanded than in Fig. 25.—27. Exine sculpture.—28. Polar view of *Vigia serrata* (Bradem et al. 8376 DAV).—29. Close-up of colpus margin (at left) and exine sculpture of *V. serrata* (Hoehne 29250 A). Scale bar: = 10 μm in Figs. 25, 26, 28; = 5 μm in Figs. 27, 29.

large grains (60–76 μm E) with an exine ca. 4–4.5 μm thick, while *P. multiglandulosa*, *P. penninervia* (Figs. 23, 24), *P. supraglandulosa* (Gillespie, 1933: figs. 7, 8), and *P. verrucosa* have medium-sized grains (39–51 μm E) with an exine ca. 2.5–3 μm . Pollen of both Type 1 and Type 2 frequently appear to have small sexinous fragments on the apertural membrane (e.g., Figs. 14, 15, 18, 20, 22).

Romanoa (Figs. 25–27). A monotypic genus

of twining woody vines endemic to southeastern Brazil.

Pollen oblate-spheroidal ($P/E = 0.91$), 54.5 μm $P \times 60 \mu\text{m}$ E, tricolpate; amb obtuse-triangular, angulaperturate; colpus broad, margins very uneven and jagged; exine tectate-perforate, 3–3.5 μm thick, gradually thinning toward the colpus margin; tectum fossulate-foveolate, surface scabrate.

Vigia (= *Plukenetia*) (Figs. 28, 29). A mono-

typic genus of vines and lianas of southeastern Brazil, now treated as a species of *Plukenetia*, *P. serrata* (Vell.) L. J. Gillespie.

Pollen suboblate ($P/E = 0.79$), $38.5 \mu\text{m } P \times 49 \mu\text{m } E$, tricolpate; amb obtuse-triangular, angulaperturate; colpus broad with margins uneven; exine semitectate-reticulate, $2.5\text{--}3 \mu\text{m}$ thick, thinner at colpus margin; muri often crenate, becoming fragmented and finely gemmate at colpus margin.

Elongate strands of sexine were observed near the colpus margin on many grains of both collections in SEM (Figs. 28, 29), but were not visible in LM.

RESULTS—SUBTRIBE TRAGIINAE

Acidoton (Figs. 30–35). Five species of shrubs in the West Indies, Central America, and northern South America. Three species were examined. Two pollen types may be distinguished based on aperture presence and exine structure.

Type 1 (Figs. 30–32). Pollen oblate-spheroidal ($P/E = 0.88\text{--}0.91$), $37\text{--}40 \mu\text{m } P \times 42\text{--}44 \mu\text{m } E$, tricolpate; amb subcircular or obscurely obtuse-triangular; colpus narrow with irregularly shaped islands of sexine, margin uneven and often indistinct; exine tectate-perforate, ca. $1.5 \mu\text{m}$ thick, uniformly thickened; tectum finely and irregularly foveolate-reticulate, lumina round to slitlike and usually narrower than the muri, muri often broken and incomplete, surface microspinulose; apertural sexine islands with surface similar to nonapertural sexine, but more irregular.

Acidoton nicaraguensis (synonym: *A. venezolanus*), the only species in Central and South America, has pollen of Type 1.

Type 2 (Figs. 33–35). Pollen spheroidal to ellipsoid-spheroidal, $37.5\text{--}41.5 \mu\text{m } S$, $40.5\text{--}44 \mu\text{m } L$, inaperturate; outline circular to broadly elliptic; exine tectate-rugulate, ca. $1.5 \mu\text{m}$ thick; rugae short to elongate, sometimes appearing beaded with slight constrictions at usually regular intervals, surface smooth, intervening perforations variable in width.

The two West Indian species examined belong to Type 2. *Acidoton microphyllus* (Fig. 35) appears to have more conspicuously beaded rugae than *A. urens* (Figs. 33, 34).

Cnesmone (Figs. 36–39). A genus of ca. 12 species of twining vines and lianas from southeastern China to the Philippines and Indonesia. Four species were examined.

Pollen spheroidal to ellipsoid-spheroidal, sometimes irregular in shape, $47.5\text{--}55 \mu\text{m } S$, $49.5\text{--}56 \mu\text{m } L$, weakly tricolpate; outline circular or elliptic, occasionally irregularly obtuse-triangular; aperture

large, elliptic in shape with margins uneven, covered with exine approximately equal in thickness to the nonapertural exine, but having a fragmented sexine; exine tectate-perforate, $1\text{--}2 \mu\text{m}$ thick, uniformly thickened; tectum punctate (i.e., having very small foveolae) and microverrucate; apertural sexine fragmented with narrow fissures separating small, irregularly shaped islands, surface microverrucate and sometimes punctate.

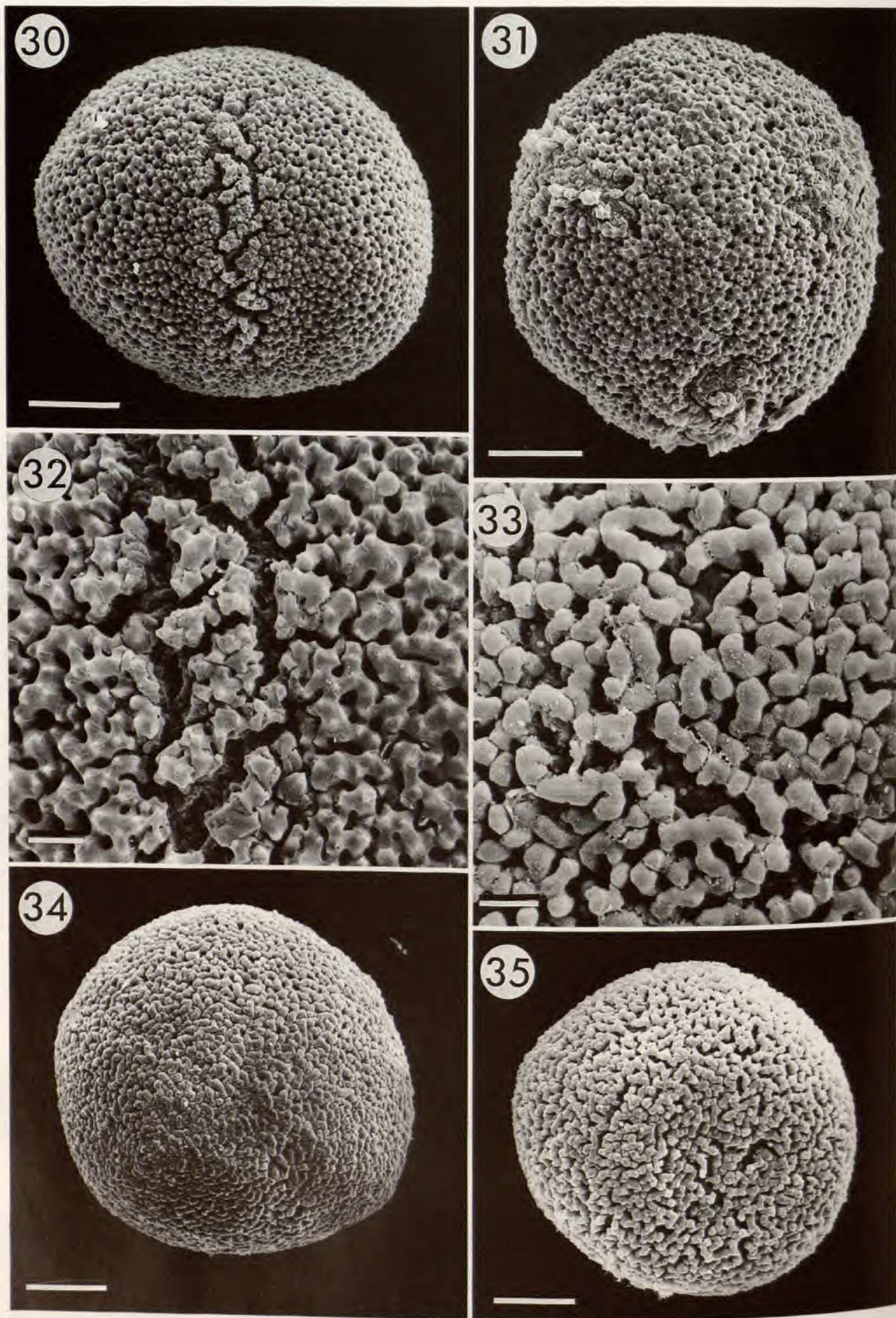
Although clearly visible under SEM, the apertures are usually not visible under LM (sometimes appearing as three less dense, more sculptured areas in optical cross section of nonacetolyzed grains, more frequently visible in acetolyzed grains). Therefore, even though the grain is aperturate, shortest and longest axes are given rather than polar and equatorial axes. The apertural sexine appears very similar to the nonapertural sexine, but is fragmented into irregularly shaped islands separated by usually narrow fissures. Typically, this weaker sexine forms three large, poorly defined colpi (Figs. 36, 39); however, apertural regions of some grains are more irregular and do not form distinct apertures (Fig. 37).

Megistostigma (Figs. 40, 41). Five species of twining vines and lianas from southeastern China to the Philippines and Indonesia. Two species were examined.

Pollen spheroidal to ellipsoid-spheroidal, $48\text{--}51 \mu\text{m } S \times 52\text{--}53 \mu\text{m } L$, weakly tricolpate, irregularly aperturate or sometimes inaperturate; outline circular or elliptic; apertural-like areas usually present, either 3(–4), large, elliptic apertures or irregularly shaped areas not forming distinct apertures; exine tectate-perforate, ca. $1 \mu\text{m}$ thick, uniformly thickened throughout; tectum punctate and microverrucate, surface often uneven; sexine of apertural-like areas fragmented into irregularly shaped islands separated by narrow branched fissures, surface microverrucate and sometimes punctate.

The areas of fragmented sexine are less dense, presumably weaker areas of exine that probably function in a manner similar to apertures. In *Megistostigma malaccense* this fragmented sexine may sometimes be absent or more commonly randomly distributed, sometimes but not always forming patterns such as rings (Figs. 40, 41, or similar to the atypical grain of *Cnesmone*, Fig. 37). In *M. cordata* these less dense areas are distributed either in the form of three (or sometimes four), large, poorly defined colpi as in *Cnesmone* (Figs. 36, 39) or in a more random pattern.

Pachystylidium (Figs. 42, 43). A monotypic genus of twining vines distributed from India to the Philippines and Indonesia.



FIGURES 30-35.³ Scanning electron micrographs of pollen of *Acidoton* (subtribe Tragiinae). 30-32. *A. nicaraguensis* (Ortiz 1104 DAV).—30. Equatorial view.—31. Polar view.—32. Close-up of colpus and exine sculpture; note presence of sexine islands on the aperture. 33-34. *A. urens*.—33. Exine sculpture showing rugae separated by fossae of variable width.—34. Grain having fossae of mostly narrow width.—35. Grain of *A. microphyllus*. Scale bar: = 10 μ m in Figs. 30, 31, 34, 35; = 2 μ m in Figs. 32, 33.

Pollen oblate-spheroidal ($P/E = 0.88-0.92$), $30.5-32 \mu\text{m } P \times 33-36.5 \mu\text{m } E$, weakly triporate; amb subcircular to obtuse-triangular, angulaperturate; aperture circular to broadly elliptic, L/W ca. 1-1.5, covered with exine slightly thinner than the nonapertural exine, but with a fragmented sexine; exine tectate-perforate, $1.5-2 \mu\text{m}$ thick, uniformly thickened; tectum punctate, microverrucate; apertural sexine fragmented into small irregularly shaped islands separated by fissures, surface microverrucate and occasionally punctate.

Pollen grains are similar to those of *Cnesmone* (Figs. 36-39), but differ in their circular apertures (Fig. 42) that are usually visible under LM as areas of slightly thinner, more sculptured exine. In addition, the apertures may sometimes appear as depressed areas under SEM (Fig. 42, aperture on right).

Platygya (Figs. 44-46). Seven species of twining woody vines endemic to Cuba. Three species were examined.

Pollen spheroidal or sometimes ellipsoid-spheroidal, $32-41 \mu\text{m}$ diam., inaperturate; outline circular to broadly elliptic, often irregularly so; exine tectate-perforate, $3-4 \mu\text{m}$ thick, uniformly thickened; tectum reticulate or rugulate with muri or rugae wider than the usually slitlike intervening perforations, surface smooth.

Platygya hexandra (Fig. 44) and *P. leonis* (Fig. 45) have a reticulate tectum with broad muri, whereas *P. parvifolia* (Fig. 46) has a rugulate tectum.

Tragia (Figs. 47-74). A genus of ca. 130 species of herbs, twining vines, and shrubs found in warm temperate and tropical regions around the world, particularly abundant in the New World and Africa. Twenty-one species belonging to two subgenera and seven sections were examined. Seven pollen types may be distinguished based on aperture condition, aperture morphology and exine structure; these types correspond closely with the infrageneric classification system.

Tragia sect. *Bia* (Figs. 47-50). Neotropical section of six species, of which *T. lessertiana* and *T. sellowiana* were examined here.

Pollen spheroidal or rarely ellipsoid-spheroidal, $49-54 \mu\text{m}$ diam., inaperturate; outline circular; exine tectate-perforate to semitectate-reticulate, $2.5-3.5 \mu\text{m}$ thick; tectum foveolate-fossulate or finely reticulate with perforations or lumina often irregular in size and shape, surface often uneven, microverrucate to densely and irregularly scabrate.

There is interspecific variation in the size of the perforations/lumina with *Tragia sellowiana* hav-

ing a foveolate-fossulate tectum (Figs. 47, 48) and *T. lessertiana* having a reticulate tectum (Figs. 49, 50).

Tragia sect. *Ctenomeria* (Figs. 51-54). Section of two species of southern Africa. *Tragia capensis* examined here.

Pollen oblate-spheroidal ($P/E = 0.89$), $31 \mu\text{m } P \times 35 \mu\text{m } E$, with 3 poorly defined apertures; amb subcircular; aperture indistinct, appearing as an elliptic depressed area covered with a layer of exine distinctly thinner than the nonapertural exine, the apertural exine sometimes splitting in an irregular manner following acetolysis; exine tectate-perforate, ca. $2 \mu\text{m}$ thick, much thinner over the aperture; tectum very finely and irregularly foveolate-reticulate, lumina subcircular and often narrower than the muri, muri thick, uneven-surfaced, sometimes broken and incomplete, surface microspinulose; apertural sexine similar to but more irregular and finer than the nonapertural sexine, sometimes irregularly fragmented.

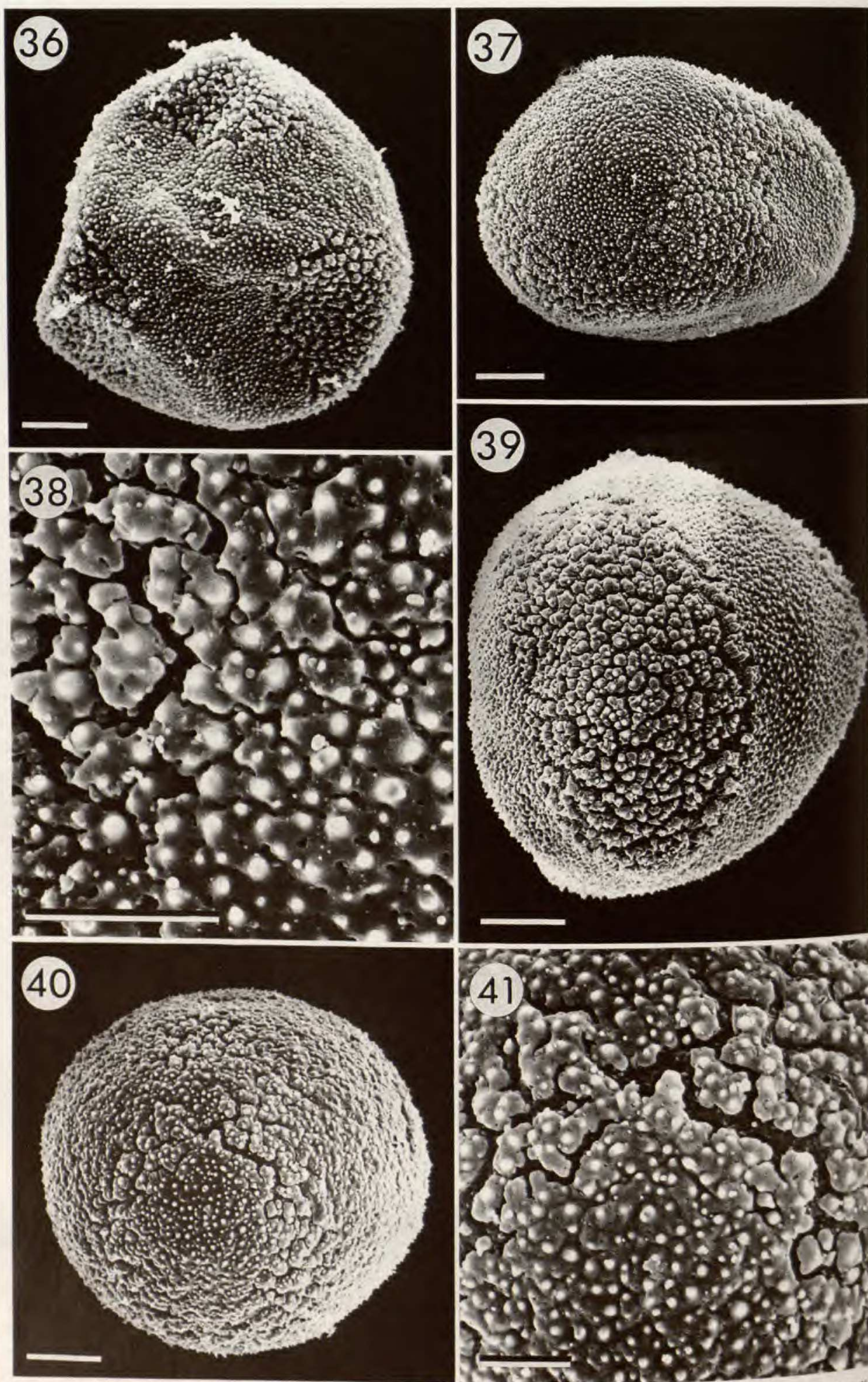
The foveolate-reticulate tectum is usually continuous over the aperture, with the aperture appearing as an elliptical depression under SEM and as a much thinner area of exine under LM. The apertures may be considered to be tenuitates, being indistinctly defined areas of thin exine (definition following Erdtman, 1952). Grains may have apertures folded inward in a direction parallel to the polar axis (Fig. 51). Following acetolysis many grains had apertures split in an irregular manner (Fig. 54).

Tragia sect. *Lassia* (Figs. 59, 60). Monotypic section of Madagascar consisting of *T. scandens*.

Pollen suboblate ($P/E = 0.86$), $33 P \times 38.5 E$, tricolpate; amb subcircular; colpus of narrow to medium width often with scattered, irregularly shaped islands of sexine, margin very uneven and indistinct; exine semitectate-reticulate, ca. $1.5 \mu\text{m}$ thick, uniformly thickened, fragmented at colpus margin; muri microverrucate to obscurely crenate; apertural sexine islands identical in sculpture to nonapertural sexine.

Tragia sect. *Leptobotrys* (Figs. 55-58). The section consists of two species of the southeastern United States; both species, *T. urens* and *T. smallii*, were examined.

Pollen oblate-spheroidal ($P/E = 0.89-0.92$), $34-37.5 \mu\text{m } P \times 38-40.5 \mu\text{m } E$, weakly triporate; amb subcircular to obtuse-triangular, angulaperturate; aperture circular to very broadly elliptic with margin indistinct, covered with a fragmented exine slightly thinner than the nonapertural exine, often split in an irregular manner; exine tectate-



FIGURES 36-41.³ Scanning electron micrographs of pollen of *Cnesmone* and *Megistostigma* (subtribe Tragiinae). 36-38. *Cnesmone anisosepala*. — 36. Polar view. — 37. Atypical irregularly aperturate grain; note that the fragmented apertural sexine does not form three apertures. — 38. Close-up of aperture margin with fragmented apertural sexine.

perforate, 1–1.5 μm thick, uniformly thickened; tectum punctate, with irregularly shaped raised areas, surface sparsely to densely microverrucate, microverrucae variable in size; apertural sexine consisting of small baculate, rounded, or conical islands, surface smooth or microverrucate.

The apertural sexine may be either continuous across the aperture (Figs. 55, aperture at top, 57) or split in an irregular manner with the underlying membrane protruding through the resulting hole(s) (Figs. 55, aperture at right, 56, 58).

Tragia sect. **Tagira** (Figs. 61–63). Section of ca. 60 species, primarily in dry areas of Africa but also found in southwest Asia. Four species examined here, *T. adenanthera*, *T. cordifolia*, *T. hispida*, and *T. involucrata*.

Pollen suboblate to oblate-spheroidal ($P/E = 0.87\text{--}0.88$), 31.5–38 μm $P \times 36\text{--}43.5$ μm E , tricolpate; amb subcircular to obscurely obtuse-triangular; colpus of narrow to medium width, often with scattered, irregularly shaped islands of sexine, margin very uneven and indistinct; exine semitectate-reticulate, 1.5–3 μm thick, usually uniformly thickened throughout, fragmented at colpus margin; muri crenate or microverrucate, often with microprojections in 1 or 2 rows; apertural sexine islands identical in sculpture to nonapertural sexine.

Tragia sect. **Tragia** (Figs. 64–66). A New World section of ca. 55 species of herbs, shrubs, and twining vines, particularly abundant in dry subtropical areas. Eight species were examined here: *T. chlorocaulon*, *T. mexicana*, *T. pacifica*, *T. petata*, *T. polyandra*, *T. ramosa*, *T. tristis*, and *T. volubilis*.

Pollen suboblate ($P/E = 0.83\text{--}0.88$), 25–37 μm $P \times 30\text{--}43.5$ μm E , tricolpate; amb obtuse-triangular, sometimes obscurely so, angulaperturate; colpus usually broad, often with 1 to several widely scattered, irregularly shaped and sized islands of sexine, margin very uneven; exine intectate?–baculate or clavate, 1.5–3 μm thick; baculae or clavae usually freestanding, but sometimes closely abutting and appearing coalesced, apex often flat, with (1–)2–4(–5) microverrucae; apertural sexine similar in sculpture to the nonapertural sexine.

The exine is generally relatively thin (1.5–2 μm) and of uniform thickness throughout, but may

sometimes be thicker (ca. 2.5 μm) at mid mesocolpium and thinner toward the aperture margins (e.g., *T. pacifica*).

Tragia sect. **Zuckertia** (Figs. 67–69). Monotypic section comprising *T. bailloniana* of Mesoamerica.

Pollen oblate-spheroidal ($P/E = 0.90$), 56 μm $P \times 62.5$ μm E , tricolpate; amb obtuse-triangular, sometimes obscurely so, angulaperturate; colpus broad with margins uneven and jagged; exine semitectate-reticulate, ca. 2 μm thick, becoming thinner toward colpus margin; tectum finely reticulate, becoming finer near aperture margin, muri scabrate.

Section unknown: *Tragia novae-hollandiae* (Figs. 70, 71). A twining vine endemic to Australia and the only species of *Tragia* represented there.

Pollen oblate-spheroidal to suboblate ($P/E = 0.88$), 36 μm $P \times 41$ μm E , with three poorly defined apertures; amb obtuse-triangular, angulaperturate; aperture circular to broadly elliptic, L/W ca. 1–1.5, with margin indistinct, covered with a fragmented exine slightly thinner than the nonapertural exine; exine tectate-perforate, ca. 1.5 μm thick, uniformly thickened; tectum punctate, with irregularly shaped raised areas, surface microverrucate; apertural sexine consisting of small, often conical or baculate islands, surface microverrucate.

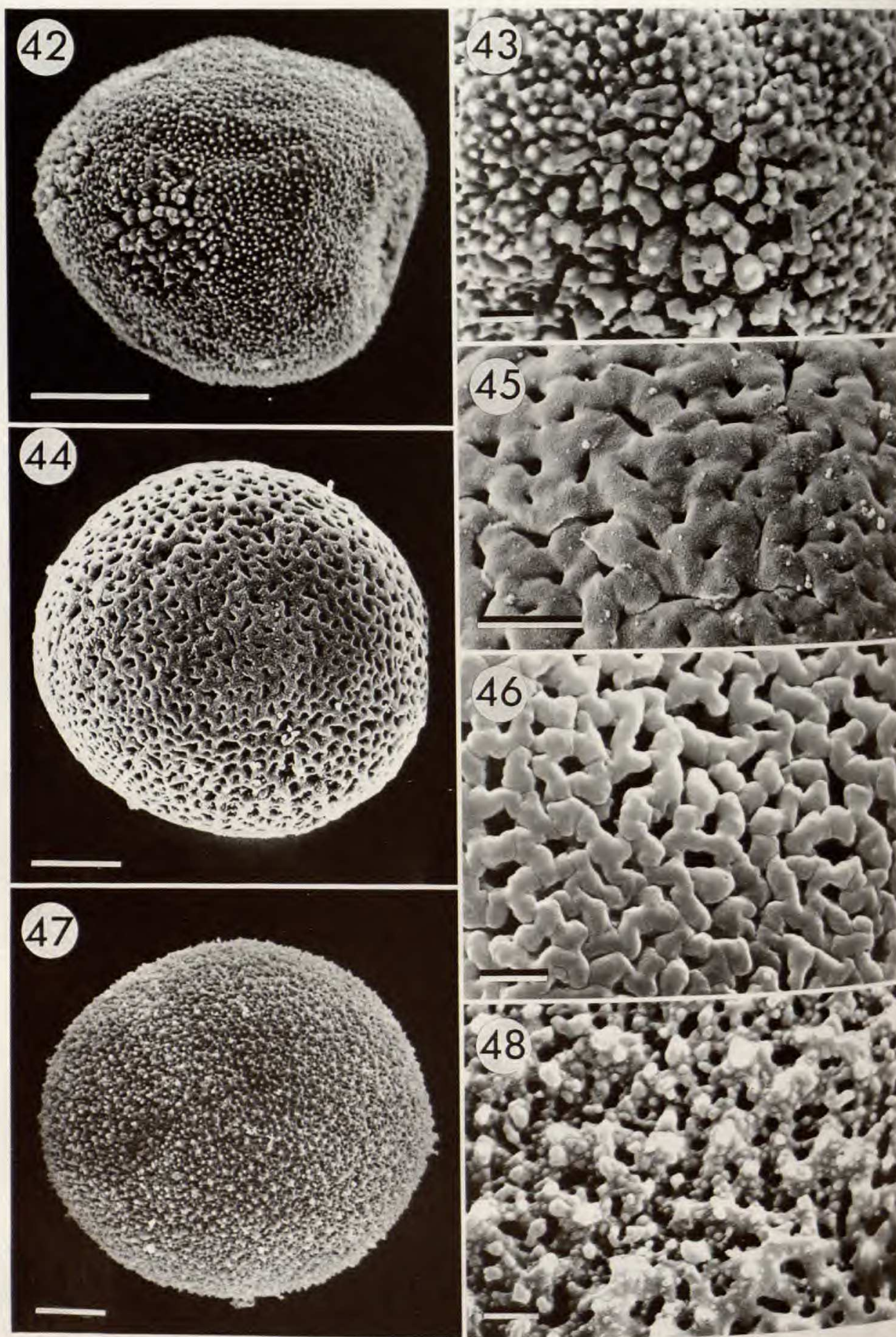
Tragia subg. **Mauroya** (Figs. 72–74). Monotypic subgenus consisting of *T. ivohibeensis*, endemic to Madagascar.

Pollen oblate-spheroidal ($P/E = 0.91$), 43.5 μm $P \times 48$ μm E , with 3(–4) poorly defined apertures; amb circular to obscurely obtuse-triangular, angulaperturate; aperture indistinct, partially covered with fragments and strands of sexine, margin very indistinct; exine semitectate-reticulate, 1–1.5 μm thick, mostly uniformly thickened; tectum finely reticulate, muri microverrucate or microspinulose; apertural sexine fragments and strands similar in sculpture to the nonapertural sexine.

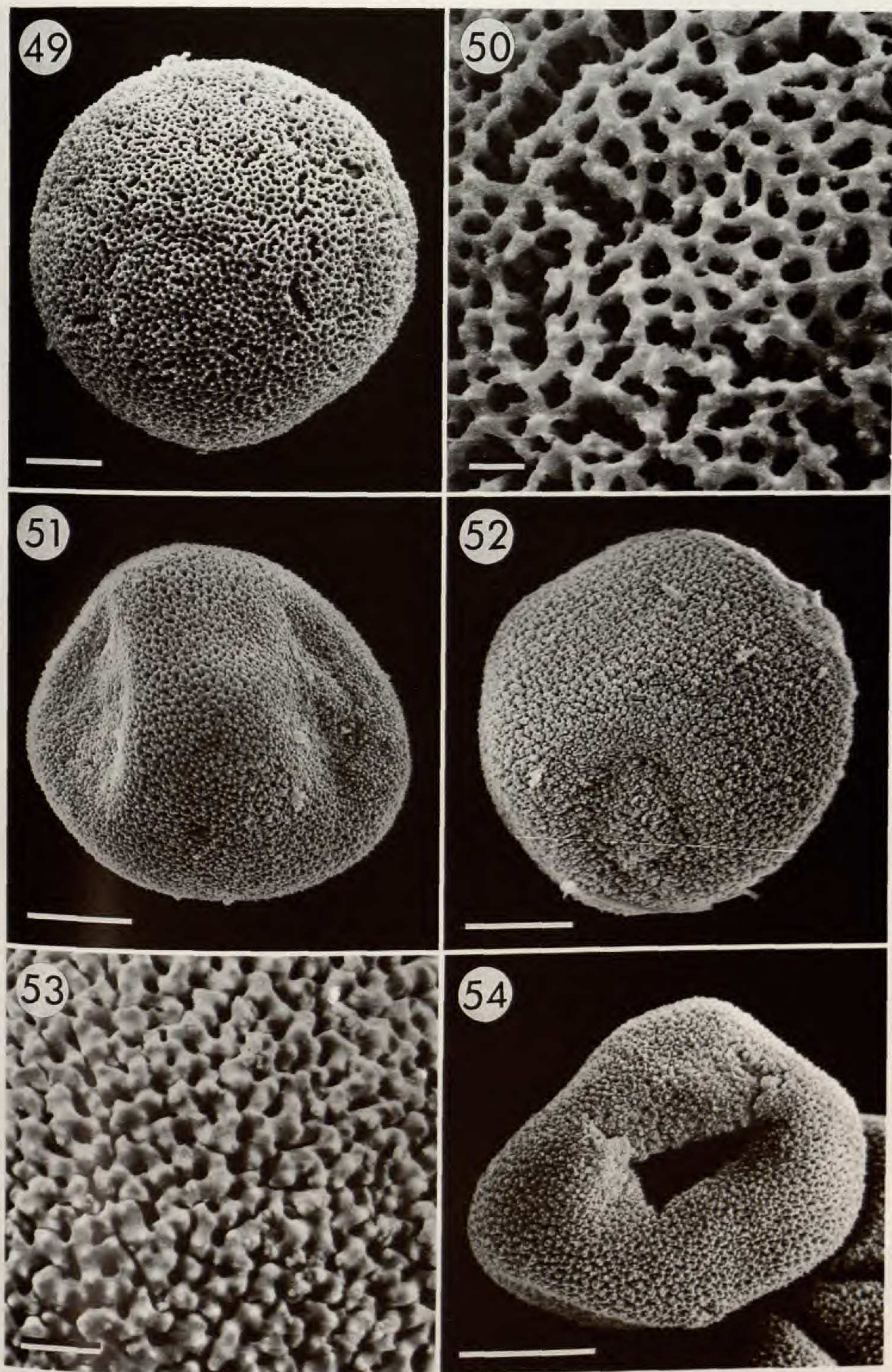
The poorly defined apertures appear to be irregular in size and shape, and are often difficult to discern in LM.

Tragiella (Figs. 75–77). Four species of twining or erect perennial herbs found in southern and eastern Africa. One species examined.

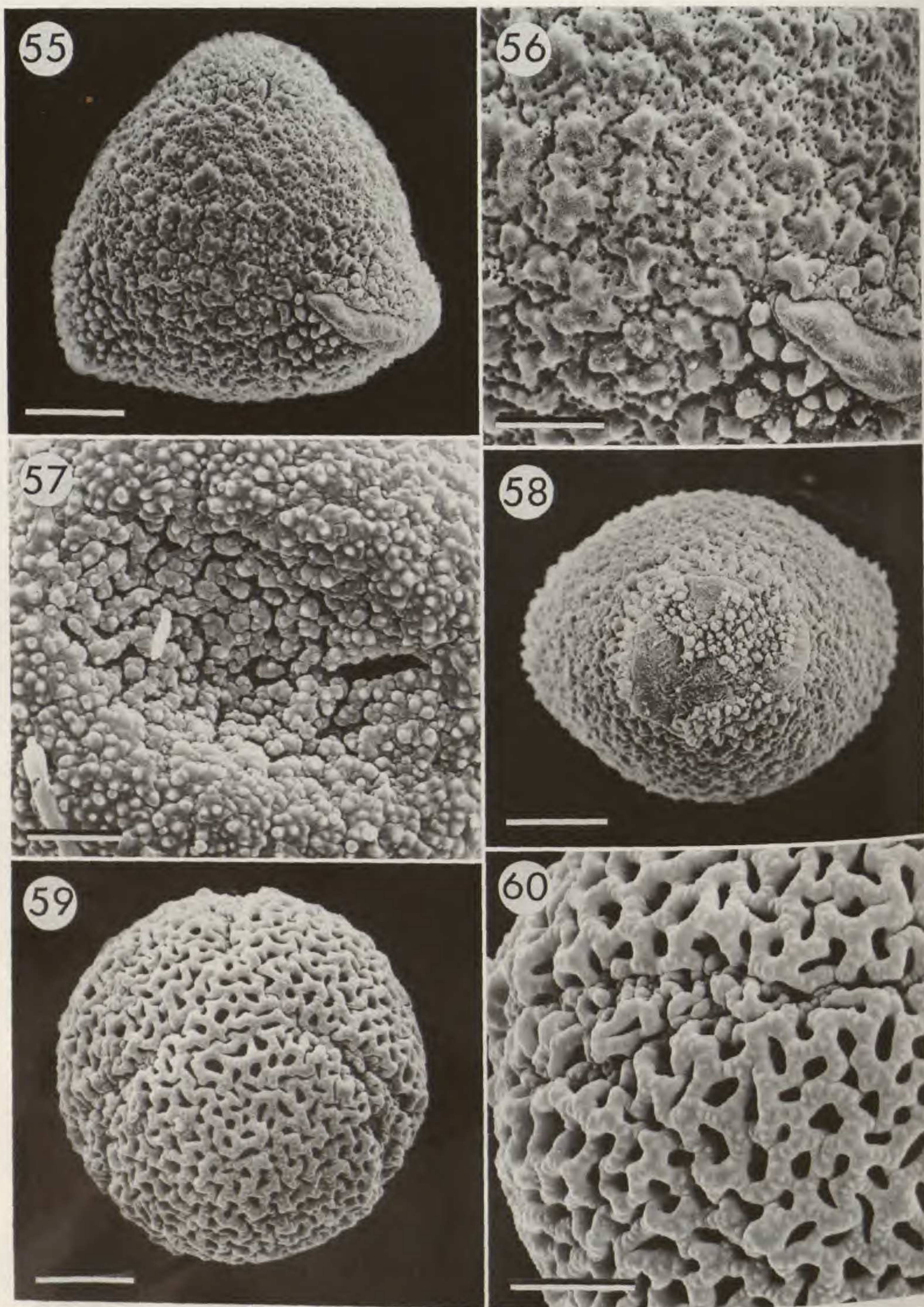
at left and nonapertural sexine at right.—39. Equatorial view of *Cnesmone tonkinensis*. 40–41. *Megistostigma malaccense* (Rahmat si Toroes 1389 A).—40. Irregularly aperturate grain.—41. Close-up showing nonapertural sexine surrounded by fragmented apertural sexine. Scale bar: = 10 μm in Figs. 36, 37, 39, 40; = 5 μm in Figs. 38, 41.



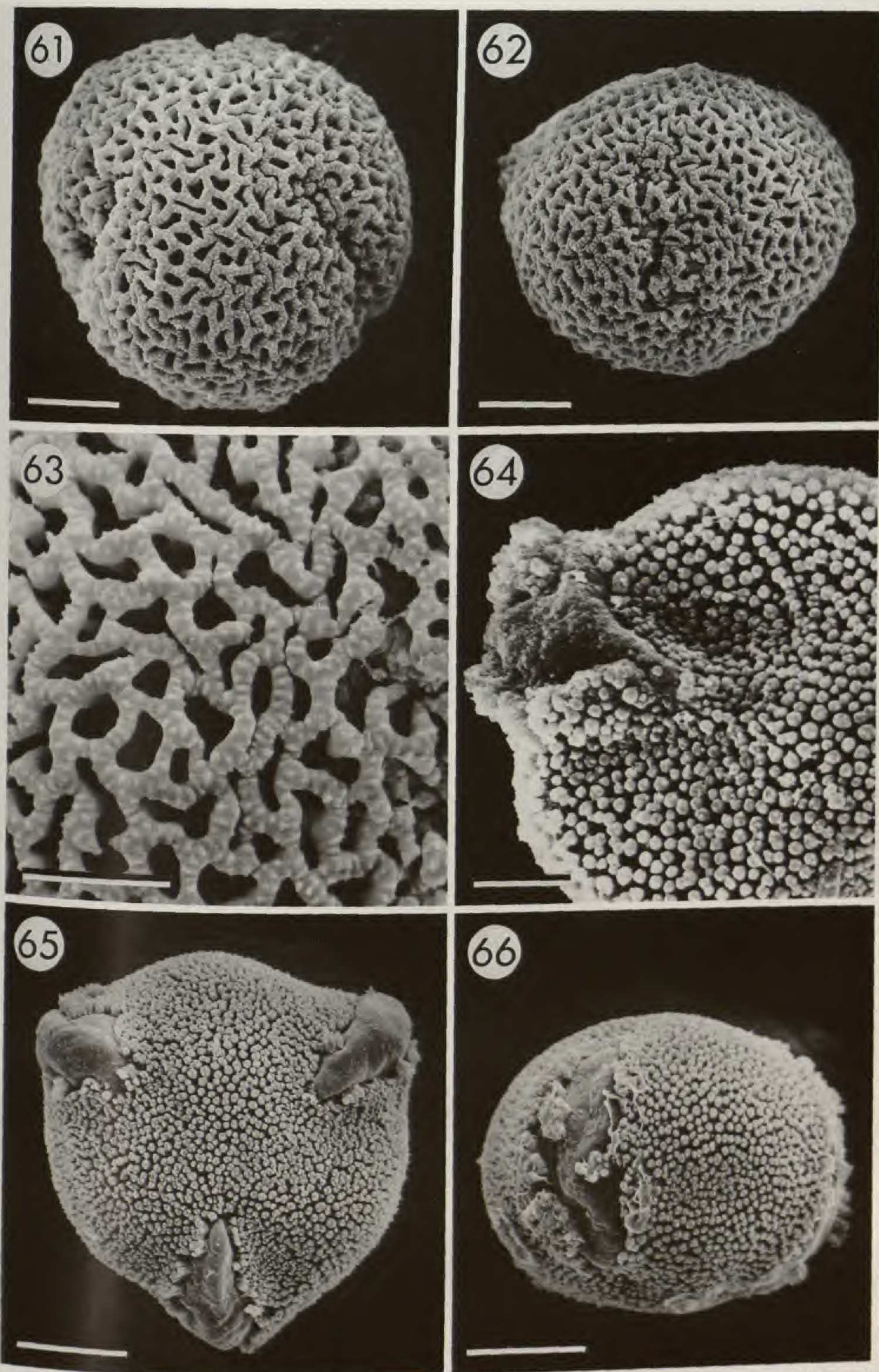
FIGURES 42-48.³ Scanning electron micrographs of pollen of *Pachystylidium*, *Platygynea*, and *Tragia* sect. *Bia* (subtribe *Tragiinae*). 42-43. *Pachystylidium hirsutum* (Ramos & Edaño 49201 UC).—42. Equatorial view showing circular apertures, with aperture at right visible as depressed area.—43. Close-up showing aperture covered with islands of sexine at bottom center surrounded by nonapertural exine.—44. Grain of *Platygynea hexandra*.—45. Exine sculpture of *Platygynea leonis*.—46. Exine sculpture of *Platygynea parvifolia*. 47-48. *Tragia* sect. *Bia*: *T. sellowiana*.—47. Whole grain.—48. Exine sculpture. Scale bar: = 10 μ m in Figs. 42, 44, 47; = 2 μ m in Figs. 43, 45, 46, 48.



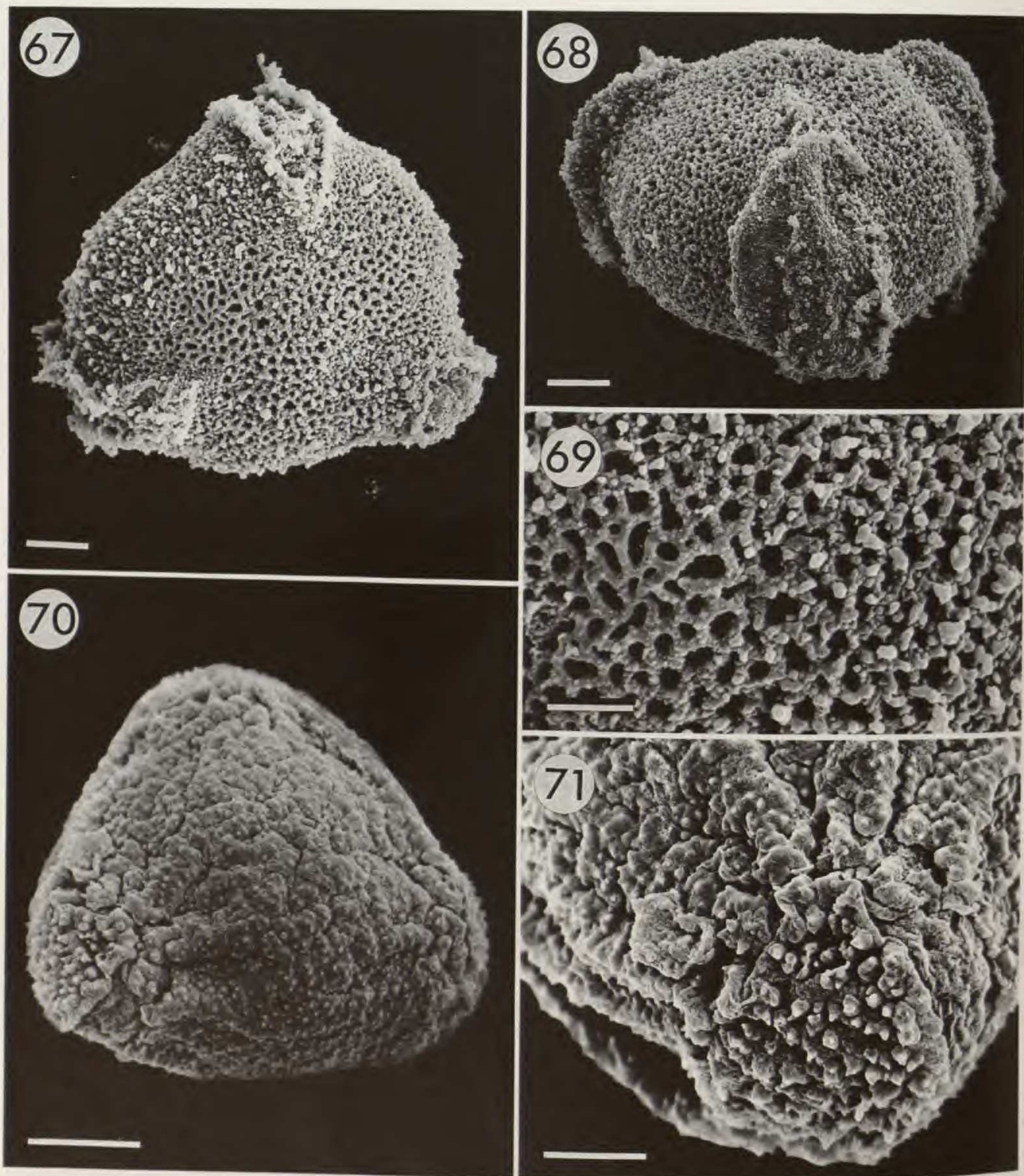
FIGURES 49–54.³ Scanning electron micrographs of pollen of *Tragia* sect. *Bia* and *Tragia* sect. *Ctenomeria*. 49–50. *Tragia* sect. *Bia*: *T. lessertiana*. —49. Whole grain. —50. Exine sculpture. 51–54. *Tragia* sect. *Ctenomeria*: *T. capensis* (Kuntze s.n. NY). —51. Equatorial view. —52. Oblique view. —53. Exine sculpture. —54. Equatorial view of acetolyzed grain with ruptured apertural exine. Scale bar: = 10 μ m in Figs. 49, 51, 52, 54; = 2 μ m in Figs. 50, 53.



FIGURES 55-60.³ Scanning electron micrographs of pollen of *Tragia* sect. *Leptobotrys* and *Tragia* sect. *Lassia*. 55-58, *Tragia* sect. *Leptobotrys*. 55, 56, 58. *T. urens*.—55. Polar view; note aperture at lower right with a split apertural sexine.—56. Close-up of aperture with split apertural sexine at lower right and nonapertural exine at upper left.—57. Close-up of *T. smallii* showing depressed circular aperture.—58. Equatorial view of *T. urens* showing circular aperture with ruptured apertural sexine. 59-60, *Tragia* sect. *Lassia*: *T. scandens*.—59. Oblique view.—60. Close-up of colpus and exine sculpture. Scale bar: = 10 μm in Figs. 55, 58, 59; = 5 μm in Figs. 56, 57, 60.



FIGURES 61-66.³ Scanning electron micrographs of pollen of *Tragia* sect. *Tagira* and *Tragia* sect. *Tragia*. 61-63. *Tragia* sect. *Tagira*: *T. adenanthera*. —61. Oblique view. —62. Equatorial view. —63. Exine sculpture with uneven and indistinct colpus margin at right. 64-66. *Tragia* sect. *Tragia*. —64. Close-up of colpus in polar view of *T. ramosa*. —65. Polar view of *T. volubilis*. —66. Equatorial view of *T. volubilis* showing colpus with scattered sexine islands. Scale bar: = 10 μ m in Figs. 61, 62, 65, 66; = 5 μ m in Figs. 63, 64.



FIGURES 67–71.³ Scanning electron micrographs of pollen of *Tragia* sect. *Zuckertia* and *Tragia novae-hollandiae*. 67–69. *Tragia* sect. *Zuckertia*: *T. bailloniana*. —67. Polar view. —68. Equatorial view. —69. Exine sculpture. 70–71. *T. novae-hollandiae*. —70. Polar view. —71. Close-up of circular aperture and exine sculpture. Scale bar: = 10 μm in Figs. 67, 68, 70; = 5 μm in Figs. 69, 71.

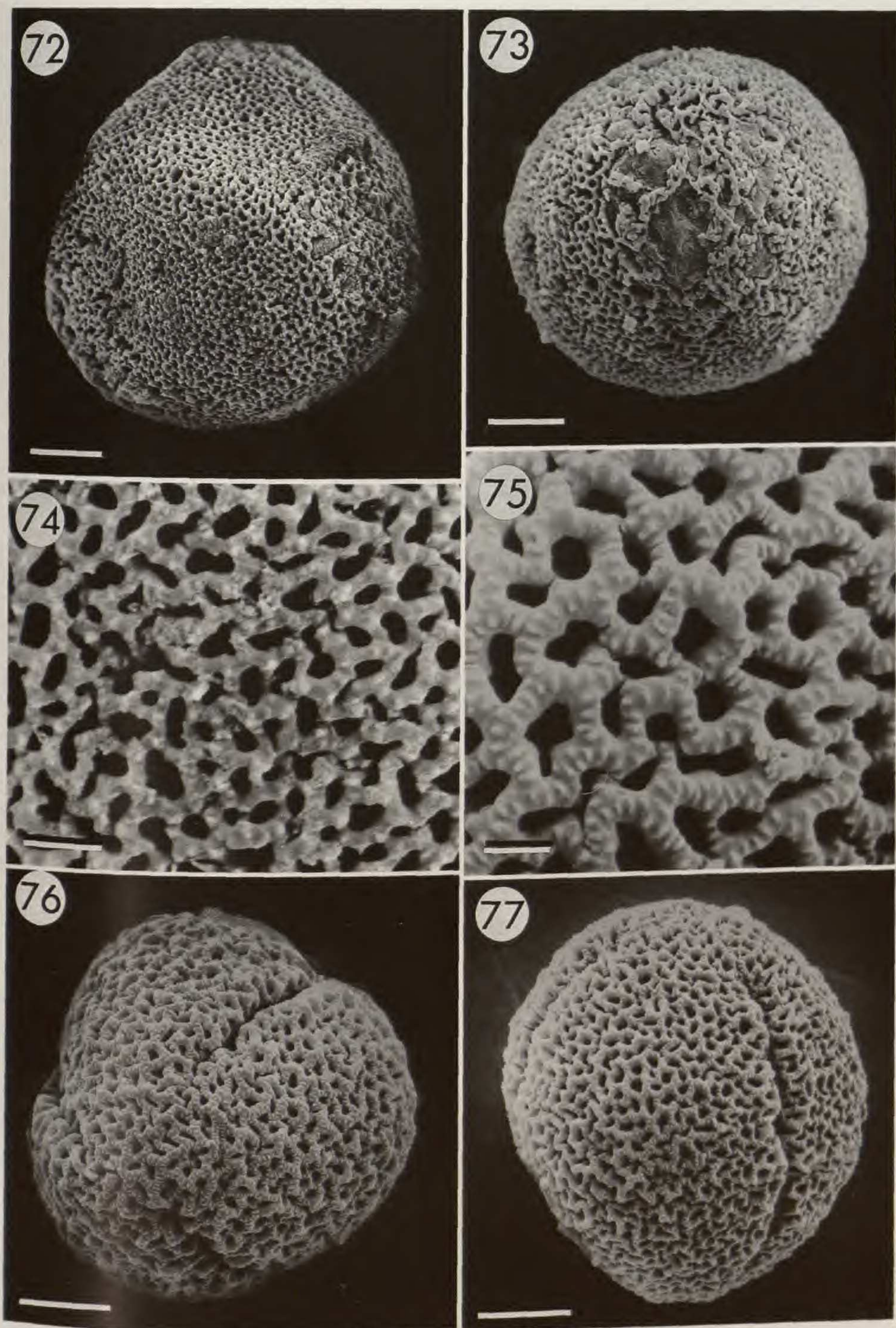
Pollen oblate-spheroidal ($P/E = 0.91$), 42.5 μm $P \times 46.5 \mu\text{m}$ E , tricolpate; amb subcircular; colpus narrow, margin very uneven; exine semitectate-reticulate, ca. 2.5 μm thick, mostly uniformly thickened; muri microverrucate or sometimes appearing crenate with transversely oblong microverrucae.

No evidence of apertural sexine islands was seen under LM or in acetolyzed pollen in SEM.

DISCUSSION

GENERAL POLLEN MORPHOLOGY OF THE PLUKENETIEAE AND PHYLOGENETIC IMPLICATIONS

A diversity of pollen morphology was found in the Plukenetieae, including tricolpate, weakly aperturate, and inaperturate pollen with exine structure ranging from tectate, semitectate, to apparently intectate (Table 2). Apertures, when present, are



FIGURES 72-77.³ Scanning electron micrographs of pollen of *Tragia* subgenus *Mauroya* and *Tragiella* (subtribe Tragiinae). 72-74. *Tragia* subgenus *Mauroya*: *T. ivohibeensis*.—72. Polar view.—73. Equatorial view showing poorly defined aperture covered with strands and fragments of sexine.—74. Exine sculpture. 75-77. *Tragiella natalensis*, acetolyzed grains.—75. Exine sculpture.—76. Polar view.—77. Equatorial view. Scale bar: = 10 μ m in Figs. 72, 73, 76, 77; = 2 μ m in Figs. 74, 75.

TABLE 2. Pollen morphology of the Plukenetieae. Aperture condition, tectum morphology (i.e., nonapertural), and presence and distribution of apertural sexine is outlined for each genus, including each section of *Tragia* and each pollen type (if more than one). The category "absent" also includes the condition of very small fragments of sexine that do not form distinct islands on the apertural membrane.

Genus	Aperture condition	Tectum morphology	Apertural sexine	Figures
Plukenetiinae				
<i>Angostyles</i>	tricolpate	finely foveolate-rugulate	absent	1-3
<i>Astrococcus</i>	tricolpate	finely foveolate-rugulate	absent—or present and continuous	4-6
<i>Eleutherostigma</i>	tricolpate	foveolate	absent	7-8
<i>Haematostemon</i>	tricolpate	finely foveolate-rugulate	absent—or present and continuous	9-13
<i>Plukenetia</i> Type 1	tricolpate	foveolate	absent	14-19
Type 2	tricolpate	reticulate	absent	20-24
<i>Romanoa</i>	tricolpate	fossulate-foveolate	absent	25-27
<i>Vigia</i>	tricolpate	reticulate	absent	28-29
Tragiinae				
<i>Acidoton</i> Type 1	tricolpate	finely & irregularly foveolate-reticulate	scattered islands	30-32
Type 2	inaperturate	rugulate	—	33-35
<i>Cnesmone</i>	weakly tricolpate	punctate	dense covering of small islands	36-39
<i>Megistostigma</i>	weakly tricolpate, irregularly aperturate or inaperturate	punctate	dense covering of small islands	40-41
<i>Pachystylidium</i>	weakly triporate	punctate	dense covering of small islands	42-43
<i>Platygyne</i>	inaperturate	reticulate or rugulate	—	44-46
<i>Tragia</i> sect. <i>Bia</i>	inaperturate	foveolate-fossulate or finely reticulate	—	47-50
<i>T.</i> sect. <i>Ctenomeria</i>	weakly 3-aperturate	finely & irregularly foveolate-reticulate	continuous but thinner, sometimes fragmented	51-54
<i>T.</i> sect. <i>Lassia</i>	tricolpate	reticulate	scattered islands	59-60
<i>T.</i> sect. <i>Leptobotrys</i>	weakly triporate	punctate, uneven-surfaced	dense covering of small islands	55-58
<i>T.</i> sect. <i>Tagira</i>	tricolpate	reticulate	scattered islands	61-63
<i>T.</i> sect. <i>Tragia</i>	tricolpate	baculate	few scattered islands	64-66
<i>T.</i> sect. <i>Zuckertiana</i>	tricolpate	finely reticulate	absent	67-69
<i>T. novae-hollandiae</i>	weakly triporate	punctate, uneven-surfaced	dense covering of small islands	70-71
<i>T.</i> subg. <i>Mauroya</i>	weakly 3-aperturate	finely reticulate	irregularly fragmented into strands	72-74
<i>Tragiella</i>	tricolpate	reticulate	absent?	75-77

simple, i.e., they lack differentiated endoapertures or ora. An unusual feature is the presence of several different types of weakly defined apertures. Invariant character states include medium to large size and suboblate to spheroidal shape (i.e., with the polar axis shorter than or equal to the equatorial axis).

The majority of Euphorbiaceae have tricolporate pollen; their compound apertures consist of an outer colpus and an inner os. Colpate, porate, and inaperturate conditions are uncommon in the family outside of the Plukenetieae except within the two subfamilies Oldfieldioideae and Crotonoideae. The Oldfieldioideae are characterized by brevicolporate or porate echinate pollen (Levin & Simpson, 1994). The Crotonoideae are characterized by the presence of a crotonoid exine structure (Nowicke, 1994), with the inaperturate condition most common and the colpate and porate aperture conditions characteristic of taxa considered by Webster (1994) to be least derived within the subfamily. Both subfamilies appear to be distantly related to the Plukenetieae on the basis of floral, vegetative, and pollen exine characters. Inaperturate pollen is not found elsewhere in the Euphorbiaceae and porate pollen is found rarely and only in distantly related phyllanthoid taxa (e.g., *Phyllanthus* L., *Hymenocardia* Wall. ex Lindl.).

The Acalyphoideae are characterized primarily by tricolporate pollen; however, there are also occurrences of tricolpate pollen outside of the Plukenetieae. These include three of five genera in subtribe Ditaxinae of the Chrozophoreae (*Argythamnia* P. Browne, *Chiropetalum* A. Juss., *Ditaxis* Vahl) characterized by tricolpate operculate pollen, subtribe Cephalomappinae of the Epiprineae (*Cephalomappa* Baill.) characterized by brevicolpate pollen, and tribe Omphaleae (*Omphalea*) having pollen resembling but distinct from *Plukenetia* (Punt, 1962; Gillespie, 1988; pers. obs.). Both the tricolpate and tricolporate aperture conditions have been described for pollen of *Adelia* L., *Lasiocroton* Griseb., *Leucocroton* Griseb. (all in tribe Adeliaeae), and *Erismanthus* Wall. ex Muell. Arg. (tribe Erismantheae) (Erdtman, 1952; Punt, 1962; pers. obs.). Subtribe Dysopsidinae of the Acalypheae (*Dysopsis* Baill.) has pollen with three weakly defined apertures superficially similar to but structurally different from *Tragia capensis* (Fernández-González et al., 1994; Suárez-Cervera, pers. comm.). Therefore, based on comparison with the remainder of the Acalyphoideae the tricolpate condition would appear to be most primitive in the Plukenetieae. Given that the most plausible direction of evolution of aperture condition in the tribe

is tricolporate → tricolpate → weakly tricolpate, triporate or 3-aperturate → inaperturate (Fig. 78), the tricolpate condition would still be considered most primitive in the Plukenetieae even if it is not homologous with the same condition in other Acalyphoideae, but was separately derived from the tricolporate condition through loss of the endoaperture.

The genus *Dalechampia* was treated as a subtribe of the Plukenetieae by Webster (1994) in his most recent classification. However, the distinctive pollen of *Dalechampia* (Punt, 1962; Webster & Webster, 1972: fig. 25) is very different from any pollen type found within the Plukenetieae (as circumscribed here, i.e., sensu Webster, 1975). Pollen of *Dalechampia* is subspheroidal to prolate, tricolporate with thickened equatorial bands of exine, and coarsely reticulate. The tricolporate aperture condition of *Dalechampia* does not support the hypothesis that the genus was derived from within the Plukenetieae as suggested by Webster & Webster (1972), given that the independent evolution of an endoaperture is a much less likely event than its loss. If *Dalechampia* is instead the sister group of the Plukenetieae, their common ancestor would presumably have had tricolporate pollen. This would imply that the tricolpate condition is a synapomorphy defining the Plukenetieae and is not homologous with the tricolpate state of other members of the Acalyphoideae.

POLLEN MORPHOLOGY AND PHYLOGENETIC IMPLICATIONS IN SUBTRIBE PLUKENETIINAE

Subtribe Plukenetiinae is relatively uniform in pollen morphology, characterized by tricolpate pollen with well defined apertures having an uneven, sometimes jagged margin (Table 2). *Plukenetia* (Figs. 14–24) has pollen with broad colpi having very uneven, jagged margins, an amb that is obtuse-triangular and angulaperturate or less often subcircular, and a foveolate or reticulate tectum. Two pollen types may be distinguished based on tectum morphology (Table 2); these types correspond approximately to groups distinguished by Punt (1962), but are more narrowly defined and restricted to *Plukenetia* (i.e., foveolate Type 1 pollen with Punt's *Plukenetia volubilis* subtype and reticulate Type 2 pollen with the *Plukenetia verrucosa* subtype). Species having Type 1 pollen may be subdivided geographically into a neotropical group characterized by large grains with a thick exine that tapers toward the margin and a paleotropical group characterized by medium-sized grains having a thinner exine that is uniformly thick or

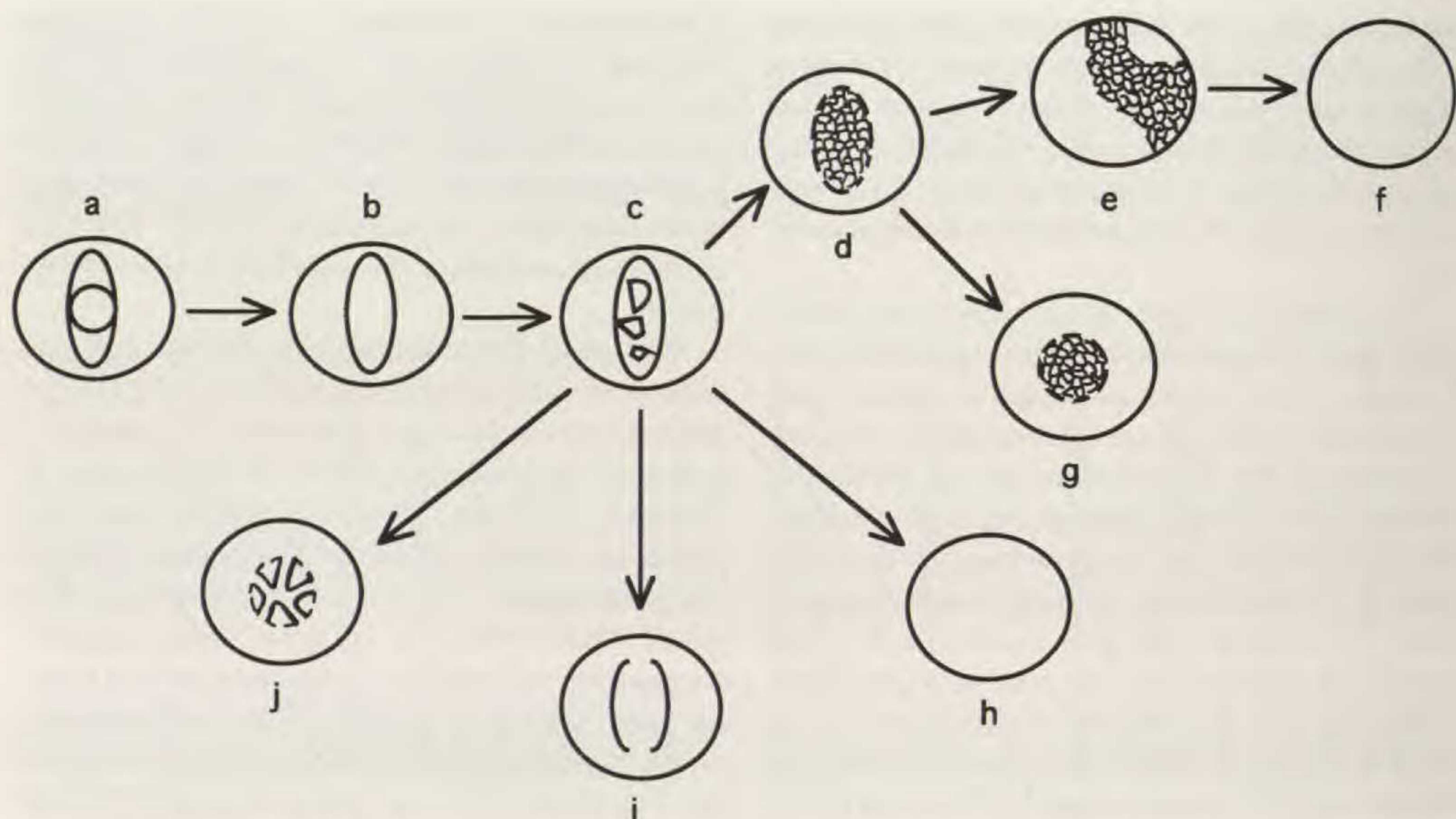


FIGURE 78.³ Evolution of aperture condition in the Plukenetieae: a hypothetical character state tree. Note that only one aperture is shown in equatorial view, and that only apertural condition is schematically illustrated, not details such as aperture margin morphology.—a. Ancestral tricolporate condition (*Dalechampia*, most Acalyphoideae).—b. Tricolpate (all Plukenetieae, *Tragia* sect. *Zuckertia*).—c. Tricolpate with scattered sexine islands on apertural membrane (*Tragia* sect. *Tragia*, *Tragia* sect. *Tagira*, *Acidoton* Type 1).—d. Weakly tricolpate, apertures with dense covering of small sexine islands (*Cnesmone*, *Megistostigma*).—e. Irregularly aperturate, apertural areas with a dense covering of small sexine islands (*Megistostigma*).—f. Inaperturate (*Megistostigma*).—g. Weakly triporate, apertures with dense covering of small sexine islands (*Pachystylidium*, *Tragia* sect. *Leptobotrys*, *Tragia novae-hollandiae*).—h. Inaperturate (*Acidoton* Type 2, *Platygyne*, *Tragia* sect. *Bia*).—i. Weakly 3-aperturate, apertural areas covered with thin layer of exine, usually visible as depressions (*Tragia* sect. *Ctenomeria*).—j. Weakly 3-aperturate, apertural areas covered with strands of sexine (*Tragia* subgenus *Mauroya*).

thicker at the aperture margin. Species having Type 2 pollen, known only from the Neotropics, may also be subdivided into two groups using the above criteria. The two pollen types and subgroups appear to have a phylogenetic basis and reflect current ideas of species relationships in the genus (Gillespie, 1993). Among neotropical species, pollen morphology, together with degree of style fusion and androecium morphology, may be used to define major species groups.

Pollen morphology of the monotypic genera *Eleutherostigma* (Figs. 7, 8) and *Vigia* (Figs. 28, 29) fits well within the range of variation found in *Plukenetia*, thus strongly supporting their recent synonymy under *Plukenetia* (Gillespie, 1993). *Eleutherostigma* has pollen of Type 1 and appears to be very closely related to the other neotropical species included in Type 1, while *Vigia* has pollen of Type 2 that is medium sized, similar to *P. verrucosa*, *P. penninervia*, and related species.

Romanoa (Figs. 25–27) also has pollen very similar to that of *Plukenetia*, but differs in its fossulate-foveolate tectum. Although morphologically very similar to *Plukenetia*, the genus may

be distinguished by its trilocular ovary and 5-parted pistillate calyx, both plesiomorphic characters in the subtribe. *Romanoa tamnoides* appears to be either the sister taxon of *Plukenetia*, which is characterized by a 4-locular ovary and 4-parted calyx, or its most plesiomorphic member.

Angostyles (Figs. 1–3), *Astrococcus* (Figs. 4–6), and *Haematostemon* (Figs. 9–13) share a very similar pollen morphology, which is distinct in colpus and tectum morphology from that of the other genera of subtribe Plukenetieae described above (Table 2). Pollen is subcircular and not distinctly triangular, with a very finely rugulate, microverrucate tectum. Colpi are narrower with an uneven but not distinctly jagged margin. The three genera share a trilocular ovary and a tree or shrub habit, very different from the vine or liana habit of *Plukenetia* and *Romanoa*. Both *Astrococcus* and *Haematostemon* have unusually thickened aperture margins with the upper and lower exine layers separating to form an elongate chamber (similar to a vestibulum). Pollen characters together with an androecium of four stamens, a unique character in the subtribe, suggest their very close relation-

ship. In contrast, *Angostyles* lacks the thickened aperture margin and elongate chamber and bears staminate flowers with numerous stamens. Thus while *Angostyles*, *Astrococcus*, and *Haematostemon* form a distinct group, the latter two are most closely related and *Angostyles* is the least derived member sharing with *Plukenetia* the plesiomorphic characters of numerous stamens and absence of an elongate chamber. Punt (1962) also remarked that pollen morphology of *Angostyles* is intermediate, sharing with *Astrococcus* and *Haematostemon* a "tectum perforatum" (as opposed to a "psilate" tectum as described for other species in the *Plukenetia volubilis* subtype), but apparently lacking a "margo" (defined as a prominent or depressed margin) as in *Plukenetia* (except *P. conophora*).

POLLEN MORPHOLOGY AND PHYLOGENETIC IMPLICATIONS IN SUBTRIBE TRAGIINAE

Subtribe Tragiinae exhibits much greater diversity in pollen morphology than subtribe Plukenetiae. Pollen is tricolpate, inaperturate, or with poorly defined apertures. Exine sculpture includes punctate, foveolate, rugulate, reticulate, and baculate conditions (Table 2). *Pachystylidium* and *Platygyne* are characterized by unique pollen types; *Acidoton* includes two distinct pollen types. The large genus *Tragia* includes seven very distinct pollen types, each characteristic of one or more sections with each section having a uniform pollen morphology.

Pollen of the West Indian genus *Platygyne* (Figs. 44–46) is inaperturate with a reticulate or rugulate tectum. No evidence was seen of small circular endexine thickenings observed by Punt (1962) on acetolyzed grains of *P. hexandra*. The generic status of *Platygyne* has been questioned (Liogier, 1971; Borhidi et al., 1973); only two floral characters, a globose or convex staminate receptacle and thickened papillose styles, separate the genus from *Tragia*. Palynologically, *Platygyne* appears to be quite distinct from *Tragia* with the exception of the neotropical section *Bia* (Figs. 47–50), the only section characterized by inaperturate pollen. *Platygyne* differs from section *Bia* in its smaller pollen grains with a coarser exine sculpture. Differences in inflorescence architecture, presence of disc segments or a globose receptacle in the staminate flowers and style morphology between these two taxa would seem to preclude a close relationship, suggesting that the similarity in pollen morphology, particularly the inaperturate condition, is due to convergence.

The genus *Acidoton* was found to contain two

distinct pollen types, differing in aperture presence and exine sculpture. The tricolpate grains of the mainland neotropical species, *A. nicaraguensis*, have colpi with uneven margins and apertural sexine islands (Figs. 30–32). The inaperturate pollen of the West Indian species (Figs. 33–35) appears more similar to pollen of its geographical neighbor *Platygyne* (Figs. 44–46), particularly to *P. parvifolia*, than to its mainland congener. Interestingly, *P. parvifolia* appears morphologically intermediate between the two genera, having an intermediate stamen number and a staminate receptacle that is glabrous like *Acidoton* but globose like *Platygyne*. This suggests that the mainland species is not the sister taxon of the West Indian species of *Acidoton*, and therefore should be treated as the distinct genus *Gitara* Pax & K. Hoffm. (as originally considered by Pax & Hoffmann, 1924). An alternative hypothesis would be the origin of the inaperturate condition from the tricolpate condition within *Acidoton*, and independently from the inaperturate condition in *Platygyne*; however, given their very similar pollen including tectum morphology, this hypothesis would seem less probable.

The three Indomalaysian genera of subtribe Tragiinae, *Cnesmone* (Figs. 36–39), *Megistostigma* (Figs. 40, 41), and *Pachystylidium* (Figs. 42, 43), form a distinct group based on pollen morphology. They are characterized by weakly defined apertures or apertural regions (sometimes absent in *Megistostigma*), a tectate-punctate exine with supratectal microverrucae, and an apertural sexine that is fragmented into small islands (Table 2). The primary differences among the genera are in the shape and size of the apertural sexine regions. *Pachystylidium* (Figs. 42, 43) has three circular, porelike apertures, whereas *Cnesmone* (Figs. 36, 39) typically has three elliptic colpuslike apertures. In *Megistostigma* (Fig. 40), the apertural condition varies from three (or four) colpuslike apertures to more randomly distributed apertural regions or sometimes inaperturate. *Megistostigma* is characterized by having an apertural condition that varies both between and within species (including within a single sample); *M. cordata* has pollen with either three colpuslike apertures as in *Cnesmone* or with randomly distributed irregular apertural regions, while *M. malaccense* is weakly and irregularly aperturate or inaperturate. Pollen evidence supports the hypothesis based on floral morphology that *Megistostigma* and *Cnesmone* are sister taxa. In fact, the two genera may not be as distinct as previously thought; the traditional distinctions of style morphology and presence of a staminate ap-

pendage appear to break down as more species are recognized and described. Pollen characters, as described above, cannot be used to separate the two genera. Since pollen of *Pachystylidium* is intermediate between pollen of *Cnesmone* and *Megistostigma* and pollen of several species of *Tragia* (*T. novae-hollandiae* and section *Leptobotrys*), pollen morphology does not strongly support either recognition of *Pachystylidium* as a distinct monotypic genus (following Pax & Hoffmann, 1919; Airy Shaw, 1969, 1975) or as a species of *Tragia* (following Webster, 1975). Pollen evidence does suggest a relationship with its geographical neighbors, *Megistostigma* and *Cnesmone*, despite a very different staminate flower morphology.

The Old World, predominantly African, taxa, *Tragia* sect. *Tagira* Muell. Arg. (Figs. 61–63), *Tragia* sect. *Lassia* (Figs. 59, 60), and *Tragiella* (Figs. 75–77) were found to share a similar pollen morphology (Table 2). Pollen is tricolpate with a reticulate tectum, a very uneven aperture margin, and scattered islands of sexine often present on the apertural membrane (apparently absent in *Tragiella*). Pollen evidence suggests that the three taxa are closely related and supports Webster's (1975) treatment of *Tragiella* as a synonym of *Tragia* (a new section within *Tragia* would be necessary to accommodate the species of *Tragiella*), rather than as a distinct genus (following Radcliffe-Smith, 1982, 1987). Section *Lassia* is morphologically very similar to *Tagira* and may not be distinct from that section; *Lassia* is distinguished by a single apomorphic androecial character. *Sphaerostylis* (not examined here) also has tricolpate pollen with a reticulate tectum similar to the above taxa according to observations by Punt (1962). This evidence is consistent with Croizat's (1941) hypothesis of a relationship with *Tragiella* (though differences in calyx and foliar morphology, as pointed out by Radcliffe-Smith (1987), would provide evidence against combining the two genera) rather than with *Megistostigma* (following Pax & Hoffmann, 1919).

Two African taxa of *Tragia* were found to have unique pollen types very different from the above African *Tragiinae*. *Tragia ivohibeensis* is an endemic Madagascan species for which Léandri (1971) created the monotypic subgenus *Mauroya*, apparently because he thought it intermediate between several genera including *Tragiella* and *Sphaerostylis*, and two sections of *Tragia*, *Agirta*, and *Ratiga*. Pollen morphology of *T. ivohibeensis* (Figs. 72–74), however, does not resemble either *Tragiella* or any species of *Tragia* examined. The apertures (usually three) are very poorly defined

areas partially covered with fragments and strands of sexine (and usually not visible under LM). The tectum, both apertural and nonapertural, is reticulate but finer than in *Tragiella* and *Tragia* sect. *Tagira*. The species appears most similar in vegetative and floral morphology to the endemic Madagascan section *Agirta*, differing primarily in style morphology. Pollen of *Tragia* sect. *Agirta* needs to be examined to confirm this suggested relationship.

The second pollen type unique among African *Tragiinae* is found in the southern African taxon *Tragia* sect. *Ctenomeria* (Harv.) Benth. While resembling the majority of African *Tragiinae* in having pinnatifid pistillate sepals (a feature found only in the Old World), the section has a very distinct androecium of numerous stamens (30–50) with highly elongate anthers. Palynologically very distinct also, section *Ctenomeria* is characterized by weakly defined apertures (*tenuitates*), which may split in an irregular manner, and a reticulate tectum, which is often continuous but much thinner across the aperture (Figs. 51–54). This pollen type is unique in the tribe and cannot be easily related to other types, emphasizing the distinctness of section *Ctenomeria*. A somewhat similar pollen type is found in the isolated, monotypic South American genus *Dysopsis* (tribe Acalypheae) (Fernández-González et al., 1994); however, similarity with *Tragia* sect. *Ctenomeria* is most likely due to convergence.

Four distinct pollen types are found among neotropical species of *Tragia*. Section *Bia* is the only section of *Tragia* characterized by inaperturate pollen (Figs. 47–50). Pollen morphology together with inflorescence architecture and staminate flowers having disc segments and five to many stamens (5–20) emphasize the distinctness of section *Bia*, as was also pointed out by Punt (1962). A second pollen type is represented by *Tragia bailloniana* (Figs. 67–69) belonging to the monotypic section *Zuckertia* (Baill.) Muell. Arg. The tricolpate pollen of *T. bailloniana* is remarkably similar to pollen of *Plukenetia* (Figs. 14–24) and *Romanoa* (Figs. 25–27), differing from *Plukenetia* Type 2 pollen primarily in its more finely reticulate tectum and muri that are often scabrate but not crenate, and from *Romanoa* only in the larger size of the perforations. Baillon (1858) originally described the species as *Zuckertia cordata* and pointed to a similarity with *Romanoa*, while Miller & Webster (1967) suggested that the species was one of the most primitive in *Tragia*. Since presence of stinging hairs and a slender 3-branched style places *T. bailloniana* in *Tragia* and not in subtribe Pluke-

netiinae, pollen evidence supports the hypothesis that the species is one of the least derived members of *Tragia*. The section *Zuckertia* pollen type appears to represent the plesiomorphic condition in subtribe *Tragiinae* based on outgroup comparison with subtribe *Plukenetiinae*.

The majority of New World species of *Tragia* belong to section *Tragia*, which appears to be characterized by a single unique pollen type. Pollen of all species examined is tricolpate with an unusual, apparently intectate sexine consisting of baculate or clavate sculptural elements (Figs. 64–66). Pollen is similar to *Tragia* sect. *Tagira* in having apertures with very uneven margins and scattered islands of sexine on the apertural membrane, but differs in exine structure and broader colpi with usually fewer sexine islands. While described as operculae by Miller & Webster (1967) on the basis of LM observations, these apertural sexine islands are irregular in shape, size, and position, and therefore cannot be considered as operculae (according to Erdtman's (1952) definition of an operculum as a "thickening of measurable bulk and clearly defined of an aperture membrane (circular in pori, elongate in colpi . . .)"). Although only eight species of this large section were examined, LM observations by Punt (1962), Miller & Webster (1967), and R. Urtecho (pers. comm.) suggest that this pollen type is characteristic of section *Tragia* and represents the only occurrence of intectate pollen (sensu Walker & Doyle, 1975, i.e., excluding the semitectate condition considered by Punt, 1962, as intectate) in the tribe Plukenetieae.

Several sections included here in section *Tragia* are sometimes treated as distinct sections (Pax & Hoffmann, 1919, 1931). These include section *Ratiga* Muell. Arg. (which includes *Tragia chlorocaulon*, *T. mexicana*, and *T. tristis*), section *Leucandra* (*T. polyandra*, *T. ramosa*), and section *Leptorhachis* (Klotzsch) Muell. Arg. (resurrected by Múlgura de Romero & Gutiérrez de Sanguinetti (1989) for several South American species, including *T. polyandra*, but treated by Pax and Hoffmann under section *Leucandra*). Since these sections share the same pollen type as section *Tragia* (sensu Pax & Hoffmann; including *T. pacifica*, *T. peltata*, and *T. volubilis*), pollen morphology does not support their recognition as distinct sections.

The fourth pollen type among New World *Tragia* is found in *Tragia* sect. *Leptobotrys* (Figs. 55–58). Pollen has three poorly defined circular apertures with a very indistinct margin and covered with small, often conical or baculate islands of sexine. The distinct apertural condition, tectum

morphology, and apertures densely covered with sexine islands support Miller & Webster's (1967) conclusions based on staminate flower morphology and LM observations of pollen that Mueller's section *Leptobotrys* is valid and should not be included in section *Tragia* (as done by Pax & Hoffmann, 1919).

Curiously, pollen of *Tragia* sect. *Leptobotrys* is most similar to pollen of *T. novae-hollandiae* (Figs. 70, 71), the only species of *Tragia* known from Australia (section undetermined; although Pax & Hoffmann (1919) included the species in section *Leucandra*, it is anomalous both in that section and section *Tragia*). The two taxa share a very similar aperture condition, tectum morphology, and obtuse-triangular shape (Table 2). Together they most closely resemble the southeast Asian genus, *Pachystylidium*, differing primarily in details of tectum morphology, both apertural and nonapertural. Airy Shaw (1969) pointed to a relationship between *T. novae-hollandiae* and *Pachystylidium* based on the shared state of subsessile anthers and suggested that the species is transitional between *Pachystylidium* and *Tragia*. In addition, *Tragia* sect. *Leptobotrys* and *Pachystylidium* share a stamen number of two, an unusual condition in the tribe. Whether similarity in pollen morphology between these three disjunct taxa is due to homology or convergence needs to be examined further.

APERTURE EVOLUTION IN TRIBE PLUKENETIEAE

Pollen synapomorphies defining the Plukenetieae are tricolpate aperture condition and uneven aperture margins. Tricolpate aperture condition is primitive in the tribe based on outgroup comparison with *Dalechampia* and the remainder of the subfamily Acalyphoideae. Throughout the Plukenetieae aperture margins are uneven and often appear fragmented, jagged, or frayed. The character state tree in Figure 78 illustrates one hypothesis of the evolution of aperture condition in the Plukenetieae, and will be discussed in greater detail below.

In subtribe *Plukenetiinae* aperture condition is uniformly tricolpate (Table 2, Fig. 78b). Variation in aperture morphology is primarily in colpus size and shape, presence of an elongate chamber within the exine next to the colpus, and presence of an apertural sexinous membrane.

In subtribe *Tragiinae* there has been an unusual radiation in aperture condition and morphology (Table 2). There is a distinct trend toward less well defined apertures and ultimately toward loss of apertures in several evolutionary lines. Aperture margins have become more irregular and less de-

fined, and fragments or distinct islands of sexine are often present on the apertural membrane.

The majority of species of *Tragia* are tricolpate; all of these species, with the exception of *T. bailoniana*, have scattered islands of sexine on the apertural membrane and very uneven margins (Fig. 78c). A single species of *Acidoton* (Type 1) also has pollen of this type.

Three different types of weakly defined apertures are found in the Tragiinae, each presumably originating independently from the tricolpate condition. One type consists of apertural areas densely covered with numerous small islands of sexine and with an exine equal in thickness or only slightly thinner than the nonapertural exine. These areas may be either elliptic (Fig. 78d; *Cnesmone*, Fig. 39, and *Megistostigma*), circular (Fig. 78g; *Pachystylidium*, Fig. 42, *Tragia* sect. *Leptobotrys*, Figs. 57, 58, and *T. novae-hollandiae*, Fig. 71), or irregular in shape (Fig. 78e; *Megistostigma*, Fig. 40). A second type of weakly defined aperture is represented by *Tragia* sect. *Ctenomeria* (Fig. 51), which has apertures covered with a continuous or sometimes fragmented, distinctly thinner exine, often visible as depressed areas (Fig. 78i). *Tragia* subg. *Mauroya* (Fig. 73) represents a third type characterized by very weakly defined apertures covered with strands of sexine continuous with and identical in sculpture to the nonapertural exine (Fig. 78j).

Inaperturate pollen appears to have evolved at least twice in subtribe Tragiinae. In the Old World, inaperturate pollen (Fig. 78f) evolved via weakly defined colpate (Fig. 78d) and irregularly aperturate grains (Fig. 78e) and is found only in *Megistostigma* (note that apertural condition is variable within the genus and within species, e.g., *M. malaccense* has both irregularly weakly aperturate and inaperturate grains, whereas *M. cordata* has both weakly tricolpate and irregularly aperturate grains). In the New World, inaperturate pollen (Fig. 78h) originated one or more times most probably from tricolpate pollen having scattered sexine islands on the apertural membrane (Fig. 78c) and is found in three taxa, *Platygyne* (Fig. 44), *Acidoton* Type 2 (Figs. 34, 35), and *Tragia* sect. *Bia* (Figs. 47, 49). An alternative hypothesis would be origin directly from tricolpate grains lacking apertural sexine islands (Fig. 78b). *Acidoton* Type 2 (and possibly *Platygyne*) pollen most likely originated from *Acidoton* Type 1, i.e., pollen having narrow colpi with numerous sexine islands, whereas there is no strong evidence either way for the origin of inaperturate pollen in *Tragia* sect. *Bia*.

CONCLUSIONS

The use of SEM in the present study of pollen morphology of the Plukenetieae has provided a much greater number of systematically useful characters than was possible with LM alone. In particular, details of tectum morphology were much more highly resolved and enabled detection of unusual apertural conditions and morphology. Several taxa, not considered to represent distinct pollen types in Punt's (1962) study based on LM alone, were distinct when viewed under SEM. These include *Tragia capensis* grouped by Punt with the *Plukenetia volubilis* subtype, *Tragiella* and *Tragia* sect. *Tagira* grouped with the *Plukenetia verrucosa* subtype, and *Acidoton* included in the *Cnesmosa* type with *Cnesmone* and *Megistostigma*.

The tricolporate, coarsely reticulate pollen of *Dalechampia* supports the hypothesis of *Dalechampia* as the sister taxon of the Plukenetieae (as circumscribed here), rather than being derived from within the tribe. Webster's (1994) treatment of the genus as a subtribe within the Plukenetieae is consistent with either hypothesis.

Pollen evidence is consistent with Webster's (1975) division of tribe Plukenetieae into two subtribes, Plukenetiinae and Tragiinae, but does not support Pax & Hoffmann's (1919) division into four informal groups. Of these groups only Astrociformes (comprising *Astrococcus* and *Haematostemon*) is monophyletic, Tragiiformes (*Tragia*) is paraphyletic, while Plukenetiiformes (most Plukenetiinae plus *Acidoton* and *Platygyne*) and Sphaerostyliformes (all other Tragiinae) appear to be polyphyletic.

Pollen morphology supports a subdivision of subtribe Plukenetiinae into an arborescent group (*Angostyles*, *Astrococcus*, and *Haematostemon*) and a lianous group (*Plukenetia* and *Romanoa*). Also supported is the recent synonymy of *Vigia* and *Eleutherostigma* under *Plukenetia* (Gillespie, 1993), and the relationship of *Astrococcus* and *Haematostemon* as sister taxa.

Subtribe Tragiinae exhibits an exceptionally diverse pollen morphology, with much of the variation present in the large genus *Tragia*. Pollen morphology, for the most part, supports the sectional classification of *Tragia*. The two largest sections, neotropical *Tragia* and paleotropical *Tagira*, have tricolpate pollen with scattered sexine islands on the apertural membrane, but are easily distinguished based on exine morphology. Of the remaining taxa, sections *Bia*, *Ctenomeria*, *Leptobotrys*, and *Zuckertia*, and subgenus *Mauroya* are

each characterized by a unique pollen type, providing evidence that they are indeed distinct natural groups. Pollen evidence does not support *Lassia* as a section distinct from *Tagira*, but does support the inclusion of sections *Leucandra*, *Leptorhachis*, and *Ratiga* within section *Tragia*. The hypothesis of section *Zuckertia* as a plesiomorphic member of *Tragia* is supported.

The remaining genera in subtribe Tragiinae, for the most part, are characterized by unique pollen types distinct from *Tragia*. The southeast Asian taxa, *Megistostigma* and *Cnesmone*, form a distinct group based on pollen morphology that is most similar to pollen of *Pachystylidium*. Pollen evidence is consistent with the status of *Platygyne* as a genus distinct from *Tragia*. *Acidoton* includes two different pollen types, inaperturate and tricolpate; the close similarity of inaperturate Type 2 pollen to pollen of *Platygyne* suggests that *Acidoton* may not be monophyletic. *Tragiella* has pollen very similar to *Tragia* sect. *Tagira*, and would perhaps be best considered a section of *Tragia* related to section *Tagira*.

Pollen and floral morphological evidence indicate that a major reorganization of generic delimitations may be necessary in the Tragiinae to better reflect phylogenetic relationships. *Tragia* appears to be a highly paraphyletic genus as presently circumscribed. Most of the remaining Tragiinae genera appear to be derived with respect to *Tragia* and defined on the basis of unusual and presumably apomorphic style and androecium characters (and also by apomorphic pollen characters). Pollen evidence frequently suggests a close relationship among geographical neighbors, a relationship that is not reflected in the current classification. To ensure a phylogenetic classification, it may be necessary to subdivide *Tragia* and recognize certain sections, such as *Bia* and *Ctenomeria*, as distinct genera (as they have been treated in the past, e.g., Baillon, 1858), since these sections are as distinct as most Tragiinae genera. An alternative but more cumbersome approach would be to combine most Tragiinae genera into *Tragia* with a complex system of subgenera and sections to indicate relationships. The level at which taxa such as *Tragiella*, *Pachystylidium*, and *Platygyne* are recognized will depend on which approach is followed.

The present study should not be regarded as exhaustive; some taxa need to be more thoroughly surveyed, particularly the two largest sections of *Tragia*, *Tagira* and *Tragia* (to verify that only a single pollen type is found in each), while several Madagascan taxa still need to be examined. The

hypotheses of phylogenetic relationships suggested in this paper need to be further tested by means of cladistic studies using floral, vegetative, and pollen characters. Taxa sharing a similar pollen morphology, but not previously thought to be closely related, need to be more thoroughly examined to determine if these similarities are homologous or the result of convergence. A more complete understanding of the phylogeny of subtribe Tragiinae is recommended prior to making specific changes in the generic and sectional classification.

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